

THE BEHAVIOURAL ECOLOGY OF YOUNG BABOONS

Frances J. Marsh

A Thesis Submitted for the Degree of PhD
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University of St. Andrews
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ABSTRACT

It is hypothesised that young baboons are potentially vulnerable to the effects of seasonal stress.

Data were collected on the behaviour of this age group during a 12 month field study of a troop of olive baboons (*Papio anubis*) on the Laikipia plateau, Kenya, using a hand-held computer and a new program written by the author. Long-term environmental records for this site were continued.

At this site there is a seasonal pattern of rainfall with inter-annual variation. Measures of biomass indicate that there are seasonal fluctuations in baboon food availability. Patterns in the occurrence of one component of the baboon's diet, *Acacia* species, are presented.

The varying behaviour of the troop as a whole is related to food availability. Differential use of the home range and observed sub-trooping behaviour are interpreted as adaptive strategies for living in a seasonal environment.

Developmental change in the behaviour associated with the mother-offspring relationship is described. Patterns in the time spent in contact with and close proximity to the mother from this site are compared with those from other sites, and striking similarities are found.

Many of the behavioural activities of infants and young juveniles, i.e. feeding, moving, types of exploring, visually attending, grooming, and receiving affiliative approaches, exhibit patterns of developmental change. Interactions between activities are examined in the context of the complete activity budget.

The effect of seasonal stress on young baboons is examined by using a technique of curve fitting. Data are compared between periods of higher and lower food availability. Significantly more time is spent feeding and less time spent in social and attending activities in the 'worst' than the 'best' months. Young baboons vary their diets seasonally. There is evidence that older infants (weanlings) are more vulnerable to the impact of seasonal stress than either young infants or young juveniles.

DECLARATIONS

(a)

I, Frances Jean Marsh, hereby certify that this thesis has been composed by myself, that it is a record of my own work, and that it has not been accepted in partial or complete fulfilment of any other degree of professional qualification.

Signed

Date 30/9/92

(b)

I was admitted to the Faculty of Science of the University of St. Andrews under Ordinance General No 12 in October 1988 and as a candidate for the degree of Ph.D. in October 1989.

Signed

Date 30/9/92

(c)

I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate to the degree of Ph.D.

Signature of supervisor

Date 30th September 1992

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ACKNOWLEDGEMENTS

I have been looking forward to writing this section for a long time. There are so many people who have helped and supported me during this four years of research, and I very much want to express my thanks and gratitude to them.

Firstly I want to thank my supervisor, Andy Whiten, for everything. We have debated curves together, and shared times of excitement over some of the results presented in this thesis - I think I also persuaded him that *Acacia* trees were interesting subjects! Particularly, he was supportive and patient when I was struggling, and it is through him that I have learnt to think and write as a scientist. Andy and Susie have fed me on numerous occasions over the years, always offering me second and even third helpings! Most of all, Andy has always been encouraging. I look forward to working with him on analysing the long-term data from Choololo in the future.

The fieldwork in Kenya on which this thesis is based was made possible by the kind permission of the Office of the President, and the support of the Institute of Primate Research, Nairobi, to whom I was affiliated.

In Kenya, there were some very special people. I am particularly grateful to John Jessel and his family for allowing me to work on Choololo Ranch and to stay at Geoffry's House. Choololo is such a beautiful place: I loved the experience of being there and will always value that part of my life. Sammy and Veronica Jessel were lovely neighbours and we shared some wonderful parties and goats! I am very grateful to Sammy for his support with day-to-day life, vehicle maintenance, for all his stories (particularly about the elephants!), and for bringing me my supplies of mail!

I am delighted to have had the opportunity of working in the field with Shirley Strum. With so much knowledge of baboons, she has insights into their behaviour that I find inspiring. Shirley made my stay in the field more comfortable by letting me share her set up, and brought chocolate brownies when she came up from Nairobi. I am particularly grateful for the encouragement Shirley has given me during the process of writing up, and I also very much look forward to discussing this work at Choololo further with her in the future.

I could not have survived in the field without the help of Francis Ngaanga King'waa, Andy Whiten's field assistant. When I first arrived, he taught me to identify the individual baboons in STT troop; he taught me about the flora and geography of the area, and in particular those plants which the baboons eat. We had some adventures together (like the time we met a lone elephant in a gully), and on several occasions he rescued me when I was had got lost or stuck! I thank him very much for all his hard work and friendship. The members of the Uaso Ngiri Baboon Project were also very supportive to me during my time in the field. Thomas Mutuku King'waa, Martin Kiio Sali, Lawrence Chege Kinyajui and Josiah Masesi Musau helped me find the baboons when they were sleeping in strange places, made me cups of chai, and generally looked after me, their 'mzungu'. I'm glad they will be able to see the end product of my time in the field, and I look forward to returning to Kenya to see them in the very near future.

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Most of all, I am very grateful for the love and support of my friends, people who have put up with me saying 'I'll be finished in the next couple of months', for the last two years, people who wrote to me in the field and kept me in touch with the rest of the world, people who have given me coffees, lunches, dinners and hugs, and listened to me whittering on about *Acacia* trees. Paul Fletcher has always been a great friend and was a huge help at the end. And especially, Mike put up with me having fits; he must be a lunatic!

The final thanks, however, go to my parents and brother. My father has been a complete hero in the last couple of weeks of this thesis preparation, proofreading and acting as an assistant in so many ways: I can honestly say that it would have taken me another month without all his help, and I thank him very much for all his patience and support. My mother has equally supported me with food parcels and words of encouragement, which have helped make this thesis finally happen. I thank them both and my brother, John, for all their love and understanding, in particular over the last four years.

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THE GUYS

Chololo, April 1990

The Foreign Contacts Adviser of *The Beast* telephoned the emporium where William was to get his kit and warned them of his arrival; accordingly it was General Cruttwell, F.R.G.S., himself who was waiting at the top of the lift shaft. ...

Before either had spoken, the General sized William up; in any other department he would have been recognised as a sucker; here amid the trappings of high adventure, he was, more gallantly, a greenhorn. ...

'I want some cleft sticks, please' said William firmly.

The General's manner changed abruptly. His leg had been pulled before, often. ... 'What the devil for?' he asked tartly

'Oh, just for my dispatches, you know.'

... 'Miss Barton will see to you,' he said, and turning on his heel he began to inspect a newly arrived consignment of rhinoceros hide whips in a menacing way.

Miss Barton was easier to deal with. 'We can have some cloven for you,' she said brightly. 'If you will make your selection I will send them down to our cleaver.'

William, hesitating between polo sticks and hockey sticks, chose six of each; they were removed to the workshop. Then Miss Barton led him through the departments of the enormous store. By the time she had finished with him, William had acquired a well-, perhaps rather over-, furnished tent, three months rations, a collapsible canoe, a jointed flagstaff and Union Jack, a hand-pump and sterilizing plant, an astrolabe, six suits of tropical linen and a sou'wester, a camp operating table and set of surgical instruments, a portable humidor, guaranteed to preserve cigars in the Red Sea, and a Christmas hamper complete with Santa Claus costume and a tripod mistletoe stand, and a cane for whacking snakes. Only anxiety about time brought an end to his marketing. At the last moment he added a coil of rope and a sheet of tin; then he left under the baleful stare of General Cruttwell.

Adapted from 'Scoop', Evelyn Waugh (1938).

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CHAPTER 1: INTRODUCTION

This thesis deals with the behavioural ecology of common or savannah baboons (the superspecies referring to *Papio anubis*, *P. cynocephalus*, *P. ursinus* and *P. papio* (Thorington and Groves, 1970)). In it, I examine the behaviour of baboons within a seasonally fluctuating environment, and in particular, the effect of seasonal stress on the behaviour of young individuals.

Before discussing seasonality, the potential vulnerability of young baboons, and the specific aims of this work, I first present some background on the diversity of environments that baboons exploit and features of baboons' adaptability.

ENVIRONMENTAL DIVERSITY AND BABOON ADAPTABILITY

Sub-Saharan Africa is composed of a variety of habitats ranging from tropical rain forest to semi-desert. These extremes are part of a continuum based on the total amount of annual rainfall and the distribution of rainfall throughout the year. Forest environments derive from high rainfall (>1500mm: Dunbar, in press) which occurs fairly evenly throughout the year, and consist of tall trees with a complete canopy; semi-desert environments consist of sparse, low-growing shrubs interspersed with patches of exposed soil, and are the result of very low and highly seasonal rainfall (Richard, 1985; Foley, 1987). Where rainfall is seasonal (semi-desert and savannah environments), plant reproduction is strongly synchronised, whereas in forest environments there is more variation because there is not the constraint of rainfall distribution.

Savannah baboons exploit the full range of these environments. They live in areas which are predominantly forest, where dense vegetation is sustained along riverine courses (Ishasha Forest: Rowell, 1966; Gombe: Packer, 1979). In contrast, they also inhabit very arid environments (Aldrich-Blake et al., 1971) and environments consisting of open or thorn-scrub savannah (Amboseli: Altmann and Altmann, 1970;

Altmann et al., 1977, 1981; Post, 1981, 1982; Gilgil: Harding, 1976; Strum, 1976, 1981; Mikumi: Norton et al., 1987; Rhine et al., 1988, 1989). Baboons also live in environments at high altitudes, for example in the Drakensberg Mountains and at Suikerbosrand, South Africa (Byrne et al., 1987; Whiten et al., 1987; Anderson, 1981, 1982). In this harsh and temperate environment, the baboons range at altitudes of up to 3000m foraging on steep escarpments in montane and sub-alpine grasslands. Baboons have also recently been observed exploiting areas where there is marked human influence (Gilgil: Strum, 1987; Forthman Quick, 1986; Amboseli: Altmann and Muruthi, 1988). At Gilgil from the late 1970s, the population of baboons studied by Strum and others learned to raid the crops of farmers who had recently started to live there, and to steal food remains from the rubbish tips of nearby institutions, thereby incorporating human food into their diet. At Amboseli, one troop of baboons ("Lodge" troop) now solely forages at one of the rubbish tips associated with the tourist lodges there. Such environments are rich in readily available, high quality foods. The productivity of this last type of environment contrasts strongly with environments such as that in the Drakensberg Mountains and in arid savannah environments.

Baboons are opportunistically omnivorous and employ a generalist feeding strategy (Post, 1981), feeding on the fruits, flowers, leaves and other parts of many different plant species, and occasionally on invertebrate and animal matter (Strum, 1975; Hausfater, 1976). They have a pseudo-opposable thumb (Napier and Napier, 1967) which facilitates a precision grip. Baboons' omnivory means that they are able to eat a wide variety of the available foods in any environment (e.g. 1 - 6 parts of 180 plant species recorded at Mikumi (Norton et al., 1987), and human foods from tip areas (Altmann and Muruthi, 1988)). The variety of their diet is enhanced by their manual dexterity which helps in gathering and processing otherwise unobtainable foods, such as underground corms and herb/grass bases, and foods which have defence structures. Also, colour vision and good manipulation enable baboons to select the most nutritious parts of food items (Altmann, 1984). Comparing the diets of baboon populations at Gilgil, Kenya, and Bole, Ethiopia, demonstrates the variety of foods eaten (as available)

in different environments: at Gilgil, blades, seeds and corms of grass species provided the bulk of the baboons' diet with fruit accounting for only a small percentage of it (Harding, 1976), where as at Bole, fruit comprised almost half of the baboons' diet (Dunbar and Dunbar, 1974).

The length of the active day is limited by the number of daylight hours, during which baboons must spend time travelling and foraging to acquire sufficient food to meet energy requirements, and also usually spend time resting and engaging in social behaviour (Dunbar and Sharman, 1984; Dunbar, in press). Time is therefore a constraint. However, savannah baboons are behaviourally flexible primates, and populations of baboons, living in environments which differ in the influences that environmental factors exert, respond to the local conditions by varying the amount of time spent in each behavioural activity. For example, using annual rainfall as a simple index of environmental conditions, time spent feeding and moving at Gombe which experiences high rainfall (1380mm) was 45.2%, and this contrasts with the 72.1% of time spent similarly in the very dry environment at Amboseli (rainfall = 225mm, 1975) (activity budget data from Dunbar, in press). In the extreme environment of the Drakensberg Mountains, baboons spent as much as 74.3% of time feeding and moving (*ibid*). Baboons are able to adapt to living in these harsher environments by spending a greater proportion of their time budget in acquiring food.

The influence of habitat quality on behaviour is clearly demonstrated in situations where some populations of baboons have access to human foods (see examples described above). Forthmann Quick (1986) reports that at Gilgil, 69.0% of time was spent feeding and moving by the troop which spent 0.7% of its feeding time eating human foods, but only 54.0% of time was similarly spent by another troop which spent much more (17%) of its feeding time eating human foods. Altmann and Muruthi (1988) report even more dramatic results from a comparison of the behaviour of a wild-feeding troop of baboons with that of a troop which habitually fed from a garbage dump: the latter group fed for only 20% of the time, whereas the former group fed for approximately 60% of the time. Both studies found that feeding on garbage tips

with their predictable sources of digestible, high carbohydrate foods, promoted inactivity. Variation in the length of the troop's day journey is another form of behavioural adaptation to different environments (see Chapter 4: Introduction).

However, the relationship between environmental conditions and behaviour is more complex than is indicated by the examples of time spent feeding and moving in different environments that have been given above. The simplification of using mean annual rainfall as an index of habitat quality is often made because of the paucity of detailed climatological or ecological data at many sites. Annual rainfall has been shown to be a reliable index of plant biomass and primary production (Coe et al., 1976; Dunbar, in press), and can be used especially when rainfall varies widely (Dunbar, 1988), but in addition to the amount of rainfall, seasonal distribution and predictability of rainfall are also important influences on habitat quality (as described above). These influential parameters of rainfall are closely related to each other, so the simplification is perhaps partially justified (Foley, 1987). Ideally, other environmental factors should also be taken into account when dealing with the relationship between habitat quality and behaviour. Dunbar (in press) used multiple-step regression equations to determine the environmental variables which affect time budget components, day journey length and group size for a sample of data from a diverse range of environments. Time spent feeding, for example, was accounted for mainly by monthly rainfall diversity (an index of seasonality) and mean ambient temperature. Dunbar related rainfall to forage quality (bush/shrub layer vegetation cover), thus forage quality could also be viewed as a factor affecting time spent feeding. Detailed analysis which includes environmental factors such as these might help to explain data where the time spent feeding/moving is higher than expected for the amount of rainfall e.g. Budongo Forest: annual rainfall = 1500mm; time spent feeding and moving = 76.9%. Other environmental factors which might explain variance in the data, and could therefore be included as environmental factors which have some influence on behaviour, are relative humidity, soil type and fertility, other geophysical aspects of the local environment (Dunbar, in press), and also the distribution of water sources (Altmann, 1974).

Seasonal rainfall distribution and the related seasonal fluctuations in resources are clearly important environmental factors which influence behaviour and how baboons spend their time in order to survive in that environment.

SEASONALITY

Seasonality can be temperate (cold winter/warm summer - high latitudes) or tropical (wet/dry - low latitudes). The Drakensberg Mountains in South Africa experience temperate seasonality, in which the stress of living at high altitude is exacerbated by seasonal low extremes of temperature and food scarcity. In central Africa, savannah environments in particular experience tropical seasonality, in which during the dry season there is no green growth and sometimes extreme resource scarcity. Most areas experience one annual cycle (e.g. Mikumi, Norton et al., 1987), but a biannual cycle is experienced in Kenya and northern Tanzania (e.g. Amboseli, Altmann, 1980). In any environment, extreme seasonality therefore extends the complex of problems that individuals in that environment have to cope with, and increases environmental stress. It has been proposed that such environmental seasonality was one of the ecological problems that early hominids had to overcome (Foley, 1987). A more detailed discussion of the nature of tropical seasonal cycles can be found in the Introduction to Chapter 3.

There are a number of different ways that animals have adapted to seasonal changes in the environment. For example, some large mammals hibernate through periods of food scarcity, but most primates do not: only the dwarf lemur hibernates through the dry season using fat reserves stored in its tail (Richard, 1985). Large herbivores such as eland and wildebeeste migrate annually to pursue continuous food and water supplies. In contrast, savannah baboons remain in the same location, where their knowledge of that area and their behavioural flexibility can help them cope with seasonal stress, although those studied in the Drakensberg Mountains were noted to retreat from the coldest and highest habitat within their range (Whiten et al., 1987).

Baboons' high dietary variety probably helps them to survive in environments

where foods become seasonally available and where there are periods of food scarcity. Post (1981) suggests that although baboons at Amboseli seemed to employ a strategy of taking advantage of peaks of production of high quality food resources, they then fed on a less diverse diet during the dry season period when many foods were less abundant. However, Hamilton (1985, 1986) and Hamilton et al. (1978) suggest that at times of decreased food availability a *more diverse* diet is selected and that at this time foods that are not normally consumed were observed being eaten. Forthman Quick (1986) notes that at the time of a drought when natural foods were scarce at Gilgil, even the troop less accustomed to feeding at the rubbish tip did so, thus incorporating additional resources. Thus, being omnivorous enables baboons to choose alternative foods when certain items are depleted (Hamilton et al., 1978), including plant species (e.g. *Euphorbia*) which are poisonous to other animals (Hamilton, 1986), and their manual dexterity allows them to acquire and process foods which are unavailable to their ungulate competitors.

Baboons' flexibility in activity budgeting is also an adaptive characteristic when living in a seasonal environment. Post (1982) found that at Amboseli the amount of time spent feeding varied throughout the year, with the greatest amount of time spent feeding in the dry season. Similarly, Dunbar (in press) has shown in his analyses of time budget data from a range of different habitats that in a highly seasonal environment (high diversity of rainfall), baboons spend more time feeding in the dry season than in the wet season. Seasonal variations in the length of day journey similarly demonstrate baboons' adaptive behavioural flexibility (see Chapter 4: Introduction).

However, while baboons can adapt behaviourally to living in many different environments (facilitated by such features as their omnivorous diet, dexterity and behavioural flexibility), there are limits to the environmental extremities in which they can survive. It would be impossible for baboons to live in such a severely seasonal environment that the increase in time necessary for feeding in the dry season was too great for a balanced time budget within the length of the limited active day (Dunbar, in

press). Dunbar discusses the idea of an 'ecologically tolerable zone', within which baboons of the *Papio* species will be able to exist by adjusting their activity budgets to meet their requirements while living in groups of at least a certain minimum size. In some environmental conditions, particularly environments which experience strong seasonality, a population of baboons may be living on a 'knife edge', where their activity budgets are stretched to the limit for the size of the group that it is necessary to have.

The complexity of the relationship between environmental factors and behaviour has already been mentioned in the previous section. Although the distribution of rainfall and related factors such as the amount of vegetation cover have been shown to be important influences on behaviour (Dunbar, in press), most pertinent, particularly when examining seasonal fluctuations in behaviour, would be an environmental variable derived from data on actual food availability. Post (1982) for example, presents data which indicate complex variations in the amount of time spent feeding during the seasonal cycle, and he stresses the need for actual food availability measures to interpret the patterns in behaviour. Rainfall is closely related to biomass and primary production as mentioned (Coe et al., 1976), but the relationship between rainfall and baboon food biomass may not be exactly similar. Few studies of primates have involved the systematic measurement of resource availability: for example, Wrangham (1977) attempted no strictly independent measures when studying the feeding behaviour of chimpanzees at Gombe, though Aldrich-Blake (1978) collected data from hectare plots to indicate spatial and temporal differences in potential food availability when studying Malaysian forest primates. Data on absolute food availability is particularly rare (Barton, 1989; and see Chapter 3 for more detailed discussion). With respect to baboon studies, at Mikumi there has been some quantitative survey of the condition of vegetation (Norton et al., 1987), but at Amboseli, Post found this too difficult (Post, 1981). The study by Byrne, Whiten and Henzi in the Drakensberg Mountains (Byrne et al., 1987, 1990; Whiten et al., 1987) and the work at Cholulu (Barton, 1989; Barton et al., 1992, in press) are the only known baboon field projects where this detailed level

of data collection has been carried out. Long-term data on absolute food availability such as that being continually collected at Cholulu, Laikipia, are therefore very important for understanding the environmental factors which influence behaviour.

The effects of seasonal stress are likely to be more critical for individuals in certain age-sex groups than for others. The activity budgets of adult females with dependent young, for example, become increasingly compressed as they have to spend more time feeding because of increased energetic demands from the feeding behaviour of their infants (baboons: Altmann, 1980; geladas: Dunbar and Dunbar, 1988) and from environmental factors which affect nutritional quality of food intake, with a cost to resting time and then finally to social time (Dunbar and Dunbar, 1988). Barton (1989) extends this and suggests that seasonal periods of low food availability probably present energy bottlenecks for pregnant and lactating females. In the most severe conditions, when critical seasonal rains fail and there is no opportunity for new growth and regeneration of food resources, drought conditions and extreme food scarcity occur which can result in the death of individuals. In Namibia, Hamilton (1985) observed the death or disappearance of 22 individuals over a period of 5 months. At Cholulu, Laikipia, there was a drought in 1987 which resulted in the deaths of about 20 individuals (about one fifth of the baboons being studied) which were mainly pregnant and lactating females and their dependent infants.

Therefore, although baboons as a superspecies can be viewed as being adapted to foraging in a savannah environment (Altmann, 1984), some individuals (e.g. pregnant and lactating females) may be particularly vulnerable to the seasonal stress that is part of the nature of this environment. Studying the behaviour of baboon individuals in a seasonal savannah environment is therefore important for the insights it provides into the relationship between behaviour and environmental constraints.

INFANT AND JUVENILE BABOONS: POTENTIALLY VULNERABLE INDIVIDUALS

Mammalian infancy has been defined as being the period until an animal "attains

the capacity to survive the death of its caretakers; generally, for primates, this means that the youngster is able to provide adequately for its own nutrition, thermoregulation and movement within the environment." (Pereira and Altmann, 1985: p225). "Juveniles are animals that would be likely to survive the death of their caretaker or loss of parental provisions ... but have not yet matured sexually" (Pereira, in press: p5). Baboons who are reaching the end of infancy or are beginning the juvenile period are those who have just become weaned from their mother, but who are not yet fully competent at foraging for food.

Pregnant and lactating female baboons' potential vulnerability to the effects of seasonal stress has been mentioned above. It is possible that older infants and young juveniles are another age group which is potentially vulnerable. Young infants still dependent on their mother's milk for nutrition are affected indirectly by the effects of nutritional stress on their mother, but weanlings who now have to acquire their own food would themselves be directly affected by seasonal stress. Information on primate mortality is scarce, but during food shortages, deaths among toque macaques on Sri Lanka were concentrated in younger age groups (Dittus, 1977, 1979). Struhsaker (1976) reports a high mortality rate for young vervet monkeys at Amboseli and attributes this to their inability to cope with a seasonally low-quality food supply. Therefore, if a period of severe seasonal stress coincides with this vulnerable period in an individual's life, then there is an highly increased risk of starvation and death for that individual.

In the last 15 years, a number of field workers studying the *Papio* species have focused on the behaviour of young baboons. However, much of the research has concentrated on the relationship between mothers and infants, and infant social behaviour, for example, the ontogeny of the mother-infant relationship, weaning behaviour and the development of independence (Ransom and Rowell, 1972; Nash, 1978; Altmann, 1980; Nicolson, 1982; Rhine et al. 1984; 1985); early social development (Ransom and Rowell, 1972; Nash, 1978); infant play behaviour (Owens, 1975); infant-adult male relationships (Ransom and Ransom, 1971; Packer, 1980;

Stein, 1984; Collins, 1986); and the triadic relationships between infants, mothers and adult male friends (Smuts, 1985; Smith and Whitten, 1988; Forster and Strum, in prep.). Older infants and juveniles (>12 months old) comprise a relatively understudied age group, and as with younger infants, research has been limited almost exclusively to aspects of social behaviour, e.g. the work by Cheney (1978a, 1978b) on the social interactions of immature male and females with other members of the troop; Johnson (1987, 1989) on rank and social relationships; and Pereira (1984, 1988) on age changes and sex differences in the social behaviour of juveniles.

Few studies have therefore focused on the behaviour of weanling and immature baboons beyond infancy, especially with respect to feeding ecology. S. Altmann has examined survivorship in terms of the diet and foraging behaviour of weanling baboons (Altmann, 1991), and Rhine et al. (1988) have looked at ecological correlates of mortality of immatures (<4 years), but this study aims specifically to examine the impact that seasonal stress, in terms of actual food availability, has on the behaviour of these potentially vulnerable individuals. Extreme seasonal stress which results in death is not experienced every year, but the non-fatal consequences of seasonal variations in the environment for the behaviour of young baboons may have important implications for adaptation and survival.

These aspects of baboon behavioural ecology were examined by studying a free-ranging troop of *Papio anubis* baboons in a seasonally fluctuating environment at Chololo on the Laikipia plateau in Kenya. The presentation of the results and the structure of this thesis are outlined below.

OVERVIEW OF THE THESIS

The main part of the thesis has 4 parts: first I describe the seasonal nature of the environment at this study site using rainfall and ecological data on actual food availability; this is followed by a section on the behaviour of the whole troop (their ranging behaviour) and how this is related to environmental seasonality; then I describe

and discuss specifically the behaviour of infant and young juvenile individuals; and finally examine the effects of seasonal periods of resource availability on the behaviour of this particular age group. In addition to the physical environment, baboons live a social environment consisting of their family and other unrelated individuals. Although data were collected on the behaviour of young baboons with respect to their proximity to adult males in the troop, it is unfortunately beyond the scope of this thesis to discuss these effects on behaviour.

Details of the study site and troop are presented in Chapter 2, along with the methods used for collecting focal animal and ecological data.

Chapter 3 presents data on the seasonal fluctuations in rainfall and biomass measures at this site. Patterns of rainfall are related to biomass and specifically to the biomass of baboon food throughout the year. Periods of resource scarcity are indicated. One component of the diet of baboons (the parts of *Acacia* species) is examined in detail, and patterns of production are related to rainfall.

Chapter 4 presents data on the ranging patterns of this baboon troop, including their differential use of areas within the home range and the occurrence of fissioning in the troop. Their ranging behaviour is related to the data on biomass, and discussed in terms of coping with the seasonal environment.

Chapter 5 deals with the relationship between mothers and their offspring. Data on the amount of time spent in contact with and in close proximity to the mother are examined with respect to developmental change, and compared to similar behaviour at other sites. Individual differences in behaviour and weaning are discussed.

Chapter 6 presents data on the behaviour of young baboons. Specifically I examine how young individuals apportion their time budgets, and how the amount of time spent in each activity changes with increasing age.

Having presented data on seasonality and the behaviour of infant and young juvenile baboons, Chapter 7 finally examines the effect of seasonality on the behaviour of this age group. This chapter reports the technique used to determine and isolate change in the behaviour of these young baboons that is associated with the course of

development, so that seasonality remained as the major factor involved in differences in behaviour. Data on the behaviour of young baboons are then examined with respect to times of high and low food availability, in order to look at the behavioural adaptations used by this age group at times of seasonal stress.

CHAPTER 2: STUDY SITE AND METHODOLOGY

LOCATION AND NATURE OF THE STUDY SITE

The work reported here was carried out on Chololo Ranch and the adjacent land. Chololo is situated on the Laikipia Plateau near Mt. Kenya, about 250km north of Nairobi and 40km north of Nanyuki (0.5 N, 36.8 E) (see Figure 2.1), at an altitude of 5300-5600 feet. Previous students from St. Andrews University have worked at this site (Barton, 1989; Lochhead, 1988), and it is also the site where Dr. Shirley Strum and the Uaso Ngiro Baboon Project (U.N.B.P.) continue to research the behaviour of two of the troops of baboons (Pumphouse Gang and Malaika) which Dr. Strum translocated to the area from Gilgil in 1984 (Strum, 1987; Eley et al., 1989).

Chololo is a privately owned ranch; the land around it to the north, south and west (Mali and Ol Jogi Ranches) is similarly managed, whereas the area to the east, the Ndorobo Reserve, is inhabited by Maasai and Samburu/Ndorobo pastoralists. The home range of the troop of baboons studied, Soitoitashe (STT), straddles the intersection of these areas and the baboons ranged freely throughout the area during the study year. Figure 2.2 is a detailed map of the study area, indicating its geography, particularly the main sleeping sites which STT used.

Barton (1989) and Barton et al. (1992) have described the geology and topography of the main study area. It is an area of approximately 50km² of undulating dry woodland and wooded and bushed grassland (following nomenclature in Pratt et al. (1966)), with occasional rocky out-crops or 'kopjes' and with *Acacias* as the predominating tree species. Barton (1989) differentiates three geovegetational areas: 1) the eastern part of Chololo Ranch and Mali Ranch to its north, which is privately owned land with fertile soils and gently rolling non-dissected plains with low ridges and smooth valleys; 2) a small area of high, steep ridges (Ndorobo Ridge) which lies at the south-east corner of Chololo Ranch and bounds the western edge of the Reserve in the southern part of the study area; 3) the Reserve proper and land owned by local people

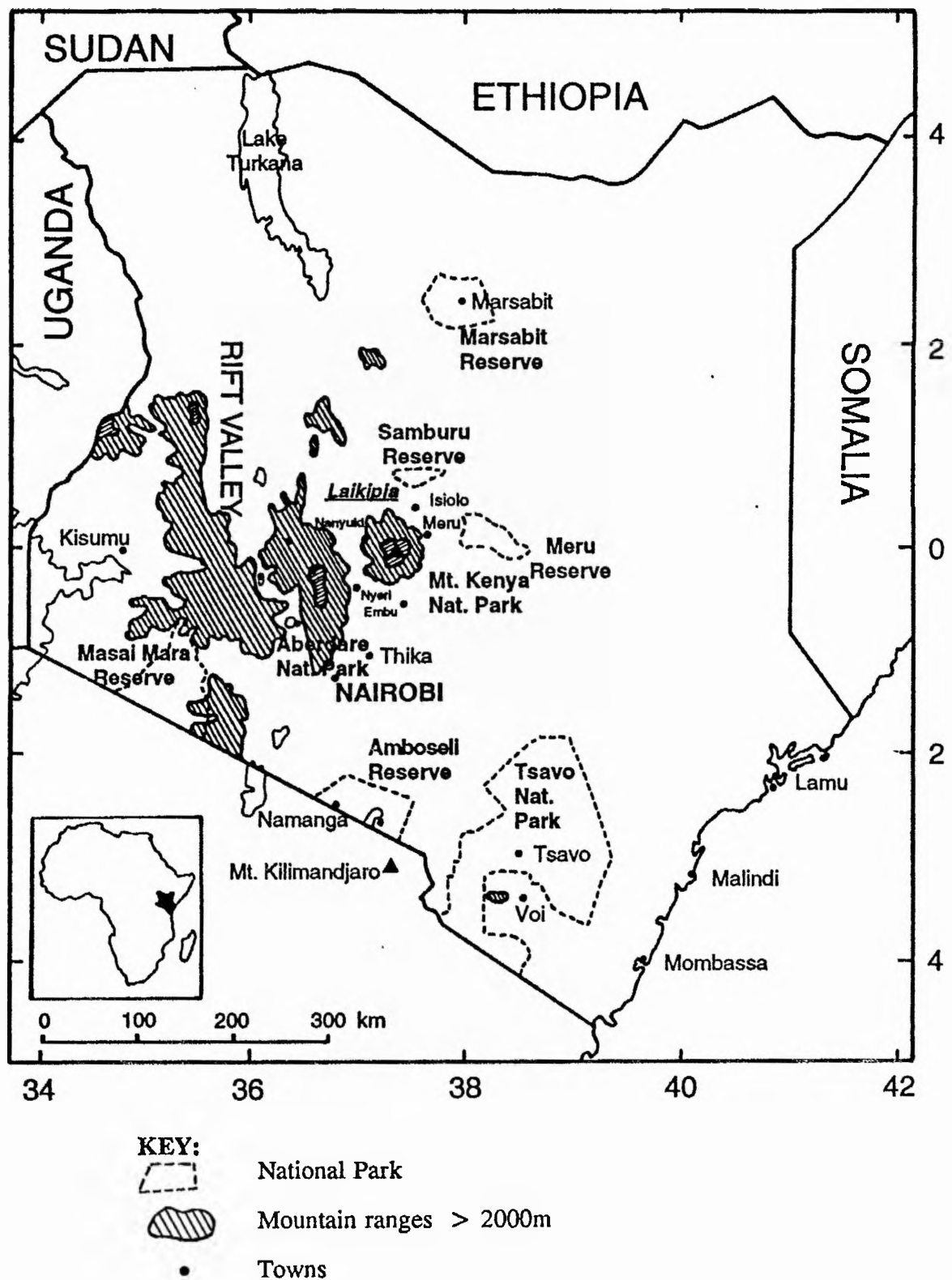
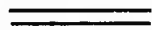
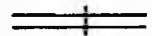
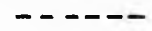


Figure 2.1: Map of Kenya showing the location of the Laikipia Plateau, near Mt. Kenya.


Figure 2.2: Map of the study area.

KEY:







ROADS AND PATHS

	Road
	Police barrier
	Track

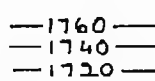

WATER FEATURES

	River
	Dam

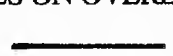

GENERAL FEATURES

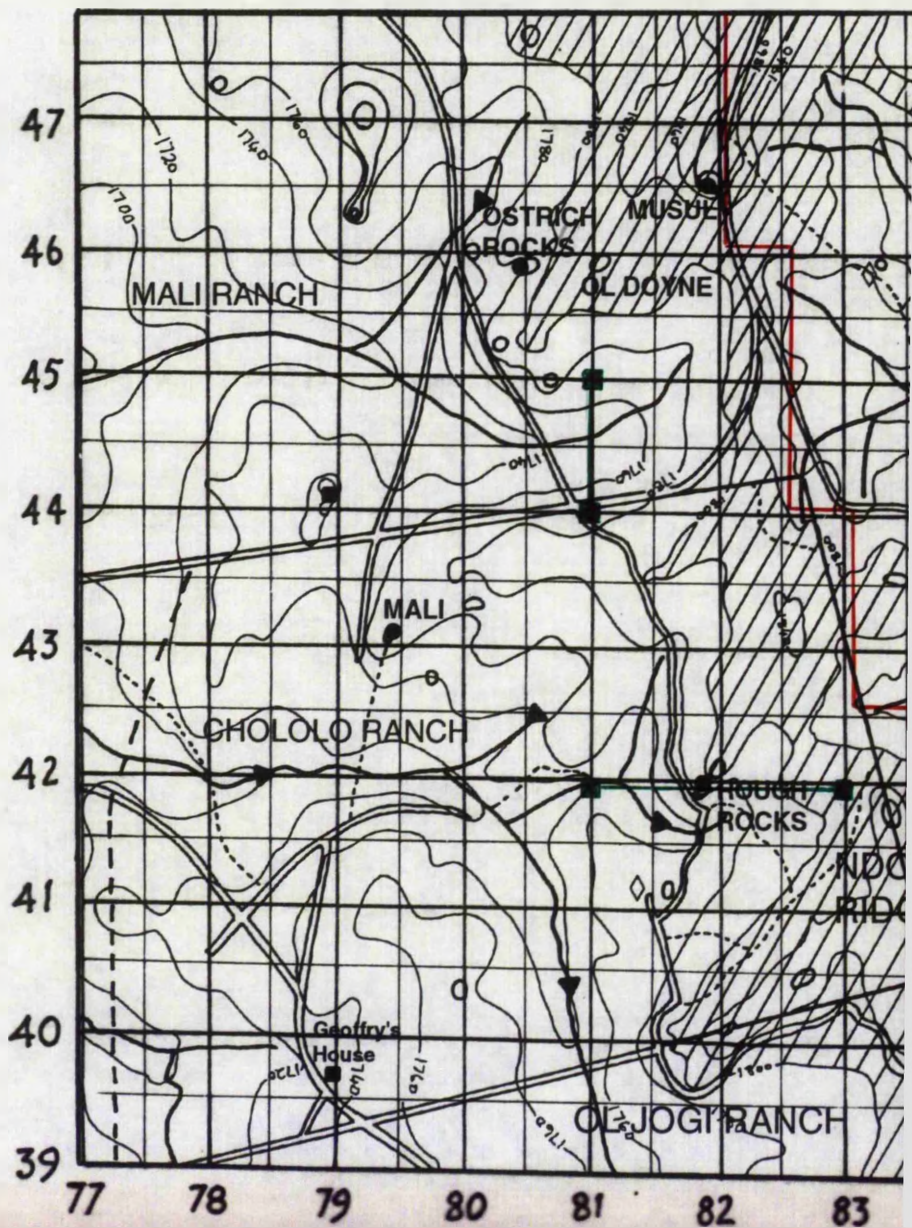
	Baboon sleeping site
	Rocky outcrop
	Building
	Local dwelling (Boma)
	Boundary line (fence posts)
	Fenceline

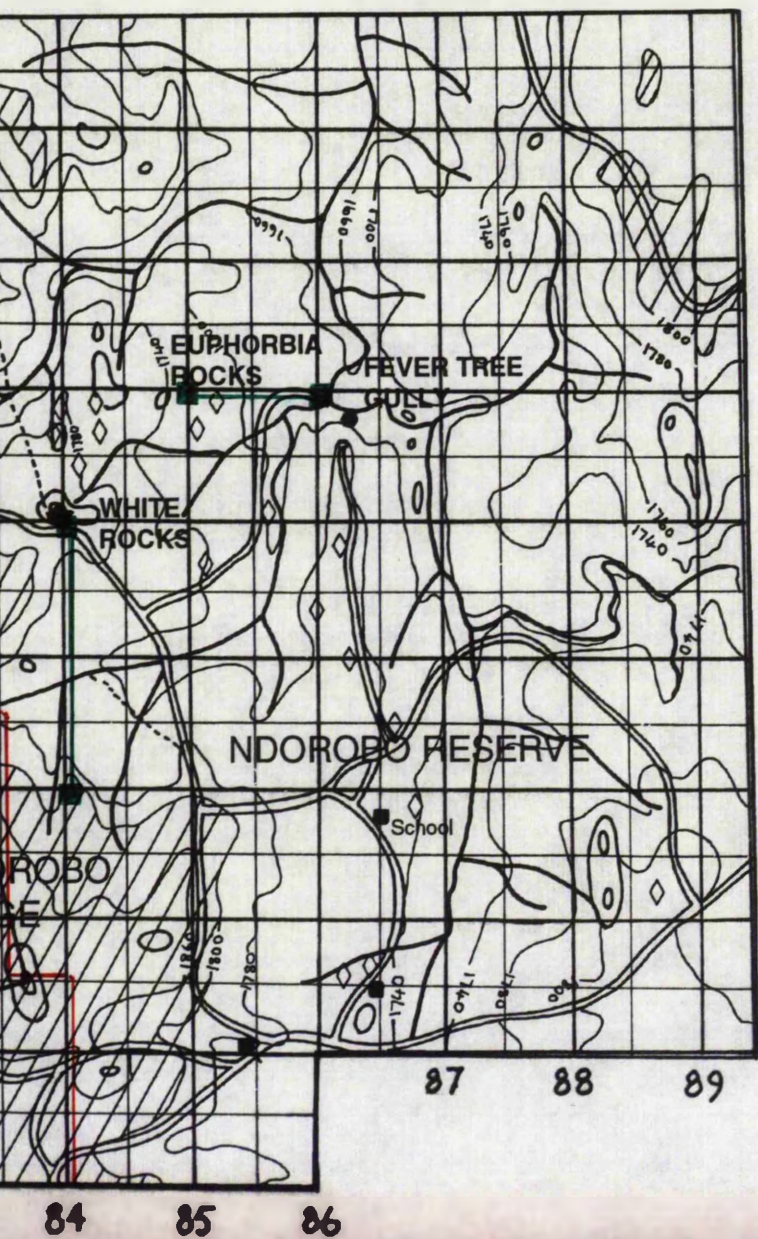
HEIGHTS

	Contours at 20m or 40m vertical interval
	Ridge above 1800m

FEATURES ON OVERLAY

	Distinction made in this study between Chololo and the Reserve
	Transects





to the north of it, an area with heavy soil erosion, arid-adapted vegetation and frequent rocky out-crops on ridges. During my study period, STT troop did not range as far south as the Ndorobo Ridge area (Barton's area 2), though they did move widely within the rest of the main study area in the Reserve and in Chololo, travelling across these non-fenced boundaries freely. For this reason I consider the main study area to be divided simply into two areas referred to as 'Chololo' and 'the Reserve'. This distinction is similar to that described by Barton but ignoring the Ndorobo Ridge as a separate area, and is based on an extension of the Chololo-Reserve boundary. The overlay of Figure 2.2 indicates this division of the study area. The topography, vegetation and other main features of both these areas are described in more detail below.

Chololo: This area comprises the western part of the study area as indicated in Figure 2.2, and is illustrated by the photograph in Figure 2.3(a). The soil on Chololo Ranch and neighbouring Mali Ranch is well drained, deep clay loam leading to high natural fertility (Barton, 1989). It is an area of gentle hills and few distinct ridges, although there are a few isolated kopjes or rocky out-crops, divided only by shallow gullies. These become seasonal water courses briefly in the rains and around them there is thicker bush. There are four places along these gullies where dams have been built, providing a nearly constant water supply for the stock on the ranches, and drinking pools for wild animal species.

Acacia etbaica is the dominant tree species with the occurrence of *A. mellifera*, *A. tortilis*, *A. sayal* (mainly around the gullies) and *A. nilotica* too. Shrubs like *Lyceum europa*, *Hibiscus* and *Grewia* species, and *Solanum incanum* are common, with plants such as *Tribulus terrestris* and *Ipomea* species (and very occasional patches of *Sansevieria intermedia*), dominating the herb layer. Grasses such as *Pennisitum*, *Erogrostis*, *Cynodon*, and *Kyllinga* species and *Tregas bertorianus* often occur in large open patches. There are also occasional clumps of the large *Euphorbia nyitae*.

Being private land, there are very few dwellings in the area and very few people on the land except for those managing it, their workers, and occasional travellers



Figure 2.3(a): Chololo: the western part of the study area.



Figure 2.3(b): The Reserve: the eastern part of the study area.

passing through. Carefully managed herds of cattle and goats are kept on the ranches, though mainly based round corrals further to the west. This area is also notable for its populations of other animals, such as zebra, giraffe, various species of antelope, cheetah, hyena, lion and occasionally elephant, as well as baboons.

The Reserve: This area comprises the eastern part of the study area (see Figure 2.2), and is illustrated by the photograph in Figure 2.3(b). Soil on the Reserve proper (bounded by En Gamendi gully to the north) and on the land owned by traditional people to the north of it has been seriously affected by water erosion and over-grazing by the herds of these local people. Hills in this area have steeper slopes than on Chololo and ridges are often marked by rocky out-crops. Gullies are deep and often steep sided yet insecure, so easily collapse, worsening the state of erosion. These gullies become seasonal water courses in heavy rain, but also contain reserves of water below the surface which are exploited by the local people who dig holes to create pools of water for themselves and their livestock. In Fever Tree Gully, there is a concrete dam built below the surface of the soil which acts to trap water sub-terraneously, so this is an especially popular place to dig water holes.

Acacia mellifera is the dominant tree species in this area (often in particularly dense thickets) though there are still numbers of *A. nilotica*, *A. tortilis* and *A. etbaica*, with *A. xanthophloea* (Fever trees) in clumps along the wider gullies. Vegetation is more arid-adapted than in the rest of the study area (Barton, 1989): there are fewer shrubs, with some *Ipomea* and *Tribulus* plants close to the ground, and an abundance of *Sansevieria intermedia* occurring in dense patches where there seems to be little else composing the herb layer. Grass coverage is patchy and sparse (exacerbated by the over grazing in this area) though there are occasional meadows of *Eragrostis*, *Cynodon* and *Kyllinga* species and *Tragus bertorianus*, especially at the sites of abandoned bomas (local dwellings) where there has been fertilisation of the area by livestock dung, and a more constant coverage of *Mariscus amauiropus*. *Euphorbia nyitae* is often found in small stands along the rocky ridges and out-crops, and there are a couple of large patches of the succulent *Opuntia vulgaris*.

The number of local people living on the Reserve can fluctuate, increasing if conditions for livestock are worse further north on the Laikipia Plateau, though most bomas are fairly permanent. Each boma has a herd of goats and sometimes a few cattle, and since these are regarded as important measures of wealth, they are accumulated rather than being managed economically, even when there is the risk of severe drought in the area. This puts a high grazing pressure on the land.

With such numbers of people and livestock on the Reserve, encounters between the local people and the baboons are unavoidable. The Reserve has a primary school and the nomadic children are encouraged to attend, but one still comes across a number of children who are kept at home in order to look after the herds of goats, and women are often moving around between the bomas or fetching water. Usually the baboons will avoid local people, especially the men in traditional dress carrying spears, and on occasions flee some distance. But they will also sometimes approach bomas, especially when food is scarce (see below). Individuals have been known to kill chickens or young goat kids and the local people naturally become very aggressive in this sort of situation. Fortunately there are no significant crops raised, so that crop-raiding, which was responsible for major human-baboon conflict at Malaika and Pumphouse groups' original habitat at Gilgil (Strum, 1987) is not a problem here. Nevertheless, some disappearances from STT and the translocated troops are suspected to be deaths resulting from attacks by local people. This is an integral part of the surroundings which comprises the home range of STT. With such human activity and numbers of goat and cattle, there are very few other animal species present on the Reserve.

The study area is not the exclusive home range of STT troop. STT2, a small troop of baboons whose members were originally part of STT until they split from the main troop in 1988, ranges in the northern part of this area. The translocated troops, Malaika and Pumphouse Gang, also have home ranges which largely overlap with that of STT, and on occasions STT has been observed sleeping at the same sites as Malaika. Since the translocation, males from these troops have emigrated into STT and vice

versa, so the increased action of STT at bomas since Barton's study year could be a result of the influence of immigrant males who are more familiar with human activity than native troops. There are also a number of other local troops which live in the study area, which STT encounter and to which males emigrate, though usually these troops avoid the observers.

Climate and seasonality:

Data on rainfall and maximum and minimum temperatures are collected daily at this site by the U.N.B.P. as part of routine long-term data collection. These data have been made available to me by Dr. Shirley Strum.

The study site falls into the category of 'dry savannah', following Delany and Happold's definitions based on annual rainfall (1979). Table 2.1 compares the mean annual rainfall at this site with rainfall data from other sites where savannah baboons have been studied, and indicates that the environment at Chololo is drier than that at many sites. Rainfall occurs seasonally in a generally biannual pattern, though there is considerable variation between years. Detailed analyses of the rainfall data from 1986 to 1990 are presented in Chapter 3 (Long-term and seasonal variation in rainfall and food availability). The mean rainfall distribution is shown in Figure 3.1, and rainfall for 1990 is presented in Figure 3.4.

There is also seasonal variation in temperature, with the greatest maximum daily temperature occurring in the dry seasons (Barton, 1989). During 1990, the monthly mean maximum and minimum temperatures varied from 20.7 to 33.6°C and from 9.1 to 13.2°C respectively, with the highest maximum temperature being 38°C.

Seasonality in the rainfall pattern influences vegetation and biomass. Analyses of biomass data are presented in Chapter 3, in particular relating fluctuations in baboon food availability to patterns of rainfall.

The seasonal environment in this area influences the behaviour of the local people, and results in increased levels of interaction between them and the baboons. As water resources become scarce in the dry season, the people defend their water pools,

Table 2.1: Comparison of mean annual rainfall at Chololo with rainfall data from other sites in Africa: data from Dunbar (in press).

SITE	RAINFALL (mm)
Budongo Forest, Uganda	1500
Gombe, Tanzania	1380
Ishasha Forest, Uganda	1292
Drakensberg Mountains, South Africa	1197
Bole Valley, Ethiopia	1105
Mulu, Ethiopia	1105
Shai Hills, Ghana	1065
Mikumi, Tanzania	734
Suikerbosrand, South Africa	700
Gilgil, Kenya (1984)	642
Awash Falls, Ethiopia	639
Metahara, Ethiopia	639
Cape Reserve, South Africa	631
Chololo, Laikipia, Kenya	628
Gilgil, Kenya (1971)	595
Amboseli, Kenya (1969)	380
Ruaha National Park, Tanzania	354
Honnet Reserve, South Africa	307
Amboseli, Kenya (1978)	225

and they and their animals travel from the Reserve on to Chololo to take the water in the dams, thereby using areas into which they do not usually go. At seasonal times of low food availability, there is also an increase in some baboons' attempts to steal food from local peoples' homes (bomas), causing them to be more often chased away.

OBSERVATION OF THE TROOP

STT is a troop of baboons (*Papio anubis*) habituated by Barton and studied almost constantly since January 1986 by students from St. Andrews and since September 1987 by Whiten's field assistant, Francis N. King'waa. Habituation was such that the troop ignored the observers' presence (see Figure 2.4), and there was minimal disturbance between the observers and the troop. Observation conditions were generally very good except in areas of thick bush or dense *Acacia* thickets or when negotiating deep gullies. Most observations were carried out at distances of between 5 and 10 metres from the baboons, and some focal data were collected from as close as 2 metres away.

Interactions between the baboons and the local people (described earlier) caused a certain antagonism between observers and the local people as we were seen as being 'responsible' for the baboons (and therefore liable to pay financial compensation!). We encouraged the people to chase the baboons away from their bomas if they saw them approaching, to try and avoid situations where the baboons were accused, correctly or incorrectly, of stealing food or killing livestock. This and the attitudes of the people made it hard to work in some areas where there were clusters of bomas, especially in the dry season, but all attempts were made to continue recording data as normal.

I began observing STT in December 1989, learning to identify the individuals in the troop and becoming familiar with the geography and ecology of the area, and continued until the end of October 1990. By March 1990 I had finalised the techniques of data collection I wished to use and in April I began to collect focal data. Demographic records were maintained during the whole period of field work, from

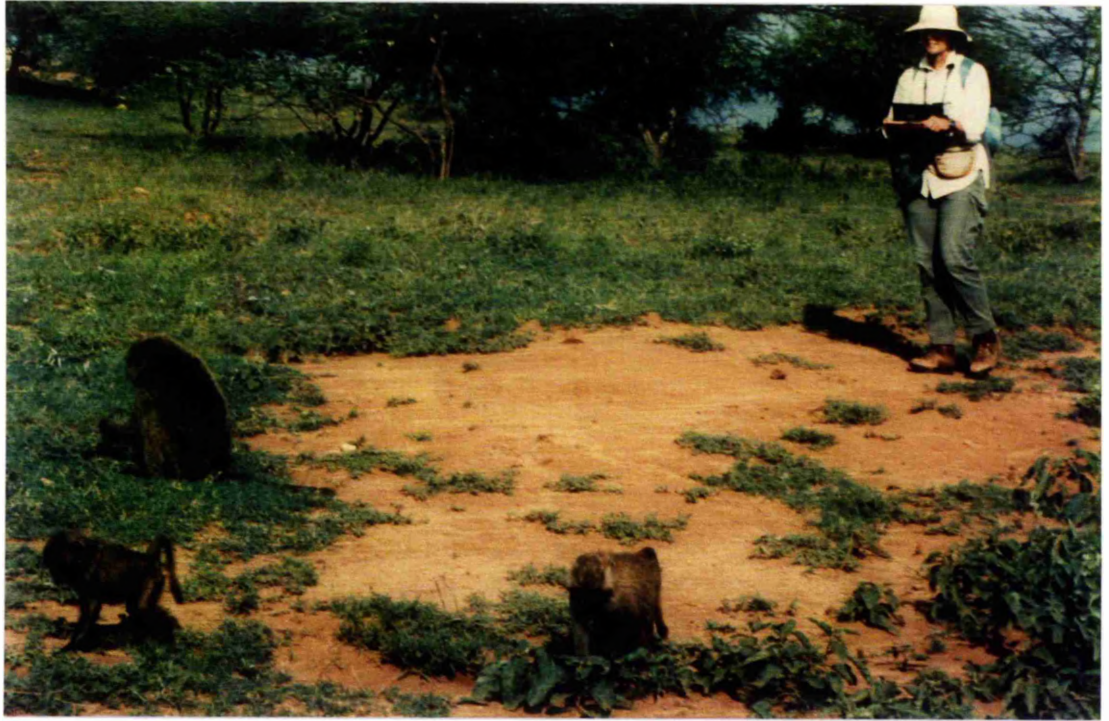


Figure 2.4: Observations were carried out at distances of 5 - 10m from the baboons; habituation was such that the troop ignored the observer's presence.

December 1989.

On days in the field, the troop was located at their sleeping site at about 0700 and followed on foot all day until they reached their sleeping site for the night, around 1800, or sometimes until the site where they were going to sleep that night was clear. Occasional 'half' days were included (0700 - 1230, or 1230 - 1800) when logistically possible with the assistance of Mr. King'waa or members of the Uaso Ngiro Baboon Project. Every effort was made to ascertain where the troop was sleeping each night, even if this just meant checking the troop's whereabouts in the evening if they had not been followed during the day.

TROOP COMPOSITION AND SUBJECT SELECTION

Table 2.2 shows the composition of STT during the period of the study (age-sex category definitions follow those used by Strum and the U.N.B.P. (see Appendix D) and Barton (1989).

'Infant' is defined as an individual younger than two years of age. Infants are described as 'black' or 'brown' depending on the colour of their hair, which changes from black to brown during development at varying rates, the transition occurring usually between 6 and 9 months of age. The category of 'juvenile' is defined differently for males and females. For females, an individual is a 'juvenile' until she is observed to start exhibiting cyclical sexual swellings (around 5 years old, Altmann et al., 1981). For males, an individual is defined as 'juvenile' until he exhibits the features of a sub-adult, noticeably longer legs, an increase of hair around the neck and shoulders and a changed shape of frame and face to more like that of an adult male (around 6 - 9 years old, Altmann et al, 1981). (See also age category definitions in Appendix D.)

For this study I denoted three age groups within the age categories described above, namely **young infants**, **older infants**, and **young juveniles**. Young infants were taken to be black infants and 'intermediates' who were in the process of turning 'brown'. Older infants were those classified as fully 'brown'. Young juveniles I define

Table 2.2: Members of STT troop, December 1989 - October 1990 (ID NAME).

* denotes focal subject; + denotes born during the study year; - denotes died during the study year.

adult male	sub-adult male	adult female	sub-adult female	juvenile male	juvenile female	infant male	infant female
GI GIL HX HURON JK JACKSON LK LARKIN OT OTIS SI STILTON TK TUSKER WE WESTLAND	DJ DJ GG GRUMPY IL ILLYIA MJ MAJOR RZ REZA YN JONAH	AL ALISON - BI BILLIE CT CATHERINE DN DONNA - EU EUPHORBIA FT FAITH KH KAHAWA KR KAREN KE KELLY LZ LIZ MD MALINDI ML MALI MR MARINA MA MAXINE NI NINA OP OPUNTIA SC SCOTTY TR TURKANA TW TWALA WT WITHANIA	AM AMANDA CN CATRINA DK DUIKER ES EUSTACIA GT GRETA JN JENNY KY KAY VS VANESSA	* EN EUSTON GD GIDEON HH HAMISI IN INDIANA JY JEREMY MI MARIO MX MAX NK NIKE * NR NIMROD SA SHASTA * TC TWITCHY TI TWIST TO TOMMY	* BE BETTY * TZ TULIZA	* CP CATERPILLAR * EI EUSI FI FIAT * KO KAZOO + * MQ MALQUALM - * NP NIPPLE + OO OTHELLO PO PISTACHIO * WG WIGGLE	+ * AH ALPHEN * BN BINTI + * DH DOUGHNUT -+ EK EUREKA + * KK KIRSTY LN LION + * MC MIRACLE * MO MAROON MT META ST SCOUT * TP TOPIC * TT TWIT + TX TUPPENCE * TY TURKEY

to be between two and four years old.

Initially I selected 15 subjects to represent these age groups (given the ages of the individuals currently in the troop). This was done using the age of the individuals at the start of April 1990, and subjects were approximately balanced for sex. Table 2.3 contains information about the subjects selected, including their age at the start of the study. For young juveniles, the youngest five individuals were chosen. Each of these juveniles had a younger sibling so it was decided to select those as subjects (though one of these siblings disappeared after one month), and other subjects were selected to maintain the sex balance. Infants born during the study period were added to the subject list when they became three months old until the total number of subjects was 18, and any subject which disappeared during the study was replaced by a closely matched individual.

Table 2.3 also details the duration of time for which focal data were collected on each subject. Figure 2.5 illustrates the ages for which focal data were collected on the subjects. As the study progressed, there was some overlap in the ages of individuals in the younger and older infant groups i.e. the oldest 'young infants' became as old as the youngest 'older infants' had been at the start of the study. For some statistical analyses of the behavioural data, subgroups of subjects were selected based on the individuals for whom data were available at similar ages (see Chapter 5: Methodology, and Table 5.1).

On the advice of Dr. Shirley Strum, I also collected focal behavioural data on adult females in the troop, and specifically the mothers of focal infants, to act as a direct comparison of activity budget and feeding behaviour, and to provide information on the troop's diet. These were chosen to include equal numbers of high and low ranking females (three of each): see Table 2.3.

Table 2.3: Details of the young infant, older infant and young juvenile focal subjects: sex (m/f); age at the start and the end of focal data collection; identity of the mother; months during which focal data were collected.

ID	SEX	AGE AT START OF STUDY (April 1990) (months)	AGE AT END OF STUDY (months)	ID OF MOTHER	MONTHS STUDIED
<u>YOUNG INFANTS</u>					
DH	f	0	7	DN*	Jul - Oct
MQ	m	0	7	MA*	Jul - Oct
KK	f	2	9	KE*	May - Oct
MC	f	4	11	ML	Apr - Oct
TP	f	7	14	TU	Apr - Oct
KO	m	7	14	KR*	Apr - Oct
<u>OLDER INFANTS</u>					
MO	f	10	17	MR	Apr - Oct
TY	f	11	18	TR*	Apr - Oct
WG	m	11	18	WT	Apr - Oct
TT	f	12	19	TW	Apr - Oct
NP	m	12	--	NI	Apr - Jun
CP	m	12	19	CT	Jun - Oct
BN ¹	f	13	20	BI	Apr - Oct
EI	m	13	20	EU*	Apr - Oct
<u>YOUNG JUVENILES</u>					
TZ	f	28	35	TU	Apr - Oct
EN	m	35	42	EU	Apr - Oct
TC	m	36	43	TW	Apr - Oct
NR	m	37	44	NI	Apr - Oct
BE ¹	f	39	46	BI	Apr - Oct

* adult females studied as focal subjects from Aug - Oct
¹ BN and BE were orphaned at the beginning of the study

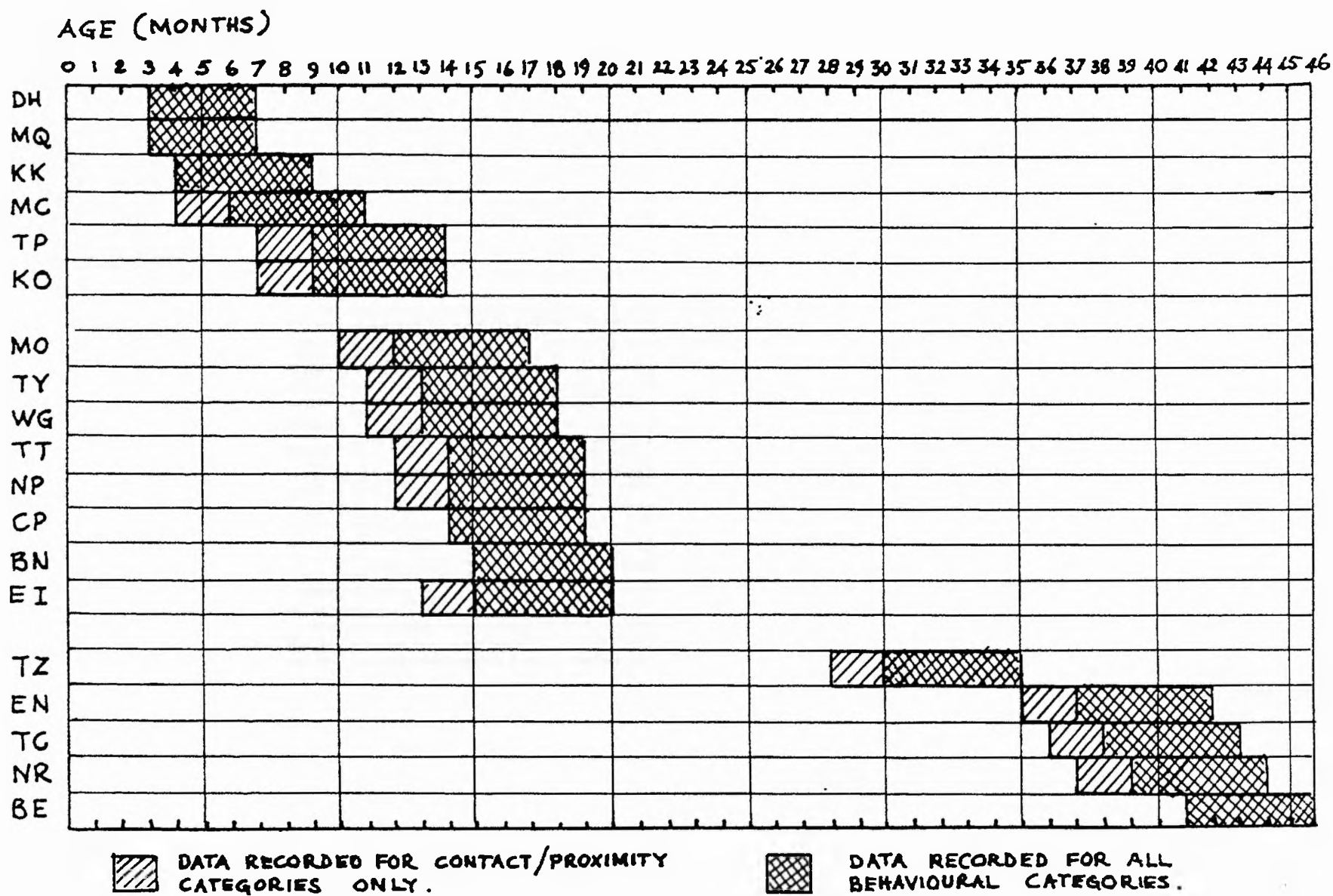


Figure 2.5: Ages for which observational data were recorded.

DATA COLLECTION

Background on the use of data collection programs and hand-held computers: the development during this study of a new program:

Since the 1950s, there have been many attempts at devising mechanical methods of recording observational data. For example, one attempt involved the use of an adapted stenograph machine which printed a 'time line' every 30 seconds on the paper tape to give a measure of time while other keys pressed by the observer represented interactive behaviours (Carter et al., 1951). Hutt and Hutt (1970) describe several devices designed as event recorders which vary in their ability to produce a continuous record of behaviour and in their portability e.g. pen recorders and automatic tape punchers. These mechanical methods, though ingenious, were not often efficient or practical, and were easily surpassed by the first desktop personal computers which were still hardly portable, but did produce easily recorded data. Particularly in the last decade, with improvements in technology, the advantages of collecting real-time behavioural data by computer have been realised.

The first computerised methods of recording such data still involved specially constructed programs and devices (for example, MORE(OS-3) and Datamyte in the U.S. (Davies, 1986) which were purpose-built event recording machines with fixed data collection programs). Often these could only be used for the project for which they were designed, meaning that isolated establishments would each be employing their own method of data collection. It was finally realised that most flexibility could be gained by using a general purpose microcomputer, in conjunction with programs which made use of the computer's internal clock and the range of keys on the keyboard to represent behavioural codes, to record real-time data (e.g. Bonsall, Zumpe and Michael, 1983). However, problems of machine portability and reliability still meant that on the whole behavioural researchers, and field workers in particular, were reluctant to abandon the old pencil-and-paper method of using check sheets, even though this resulted in hours of transcribing the data into a computer-readable form for

analysis.

In the 1980s, reduced size and increased portability of microcomputers and their easy availability on the market, encouraged some workers to think further about using computers to collect data in non-laboratory situations. Among the first advances in this area were the programs written by Felce (1986) and by Browne et al. (1984) for the Epson HX-20 portable computer, and the programs written by Whiten and Barton (1988) to be run on Hewlett-Packard's hand-held HP-71 computer. Felce's program 'Behaviour' was written to record staff-client behaviour in homes for the mentally handicapped, and Browne's set of programs entitled 'Ethogram' were used to collect data on mother-infant interactions in a study of child abusing families in their own homes: both projects were carried out successfully. Barton and Whiten used their programs to collect focal animal behaviour studying savannah baboons in the field (Barton, 1989; Barton and Whiten, in press). Other workers (e.g. Unwin and Martin, 1987; Lopez-Lujan and Mondragon, 1988) have also recently recognised the advantages of using non-specialised micro-computers and simply written programs as behavioural event recorders.

However, these programs are written in BASIC programming languages, and so are machine dependent, which is a limitation at a time when continual improvement of hardware means machines are quickly made redundant and software has to be rewritten. An attempt at writing a flexible data collection program which could be run on any micro computer was 'MINKEY' (Marsh, 1988), written in PASCAL. PASCAL is a more sophisticated programming language which allows the writing of complex programs which are then compiled, making them fast and machine independent. This program was tested and used on a Toshiba T-1000 portable computer by postgraduate researchers at Durham University (Dagnan, pers. comm.). An extension of this work is the computer program 'MBUNI', which was developed during the present study. 'MBUNI' provides a particularly flexible method of collecting real-time behavioural data for any research project (rather than just one particular project), and is similarly non-machine specific. Data are stored in a standard form which can be used in

statistical packages and databases without the need for transcription or alteration, so as the capabilities of such analytical packages similarly improve, the output from using 'MBUNI' will not be constrained. (Similar flexible computer programs and packages have become available on the market since the start of this study e.g. Stirling Microsystems: 'Time and Event Logging on the Psion' software package; Noldus: 'The Observer'.)

The last couple of years have seen new developments in the capabilities of the small personal computers which are available, and increased affordability. In 1989, DIP Ltd. designed a 6" x 3" hand-held computer with a 8 x 40 screen ('Portfolio') which has a simulation of the operating system which all IBM-compatible microcomputers use (MS-DOS), and so is capable of running machine independent, compiled programs. To date, this is the most compact portable PC which can run this type of data collection program, and so was chosen to be used together with 'MBUNI' during this research.

Features of 'MBUNI':

'MBUNI' is a new program for recording focal animal behaviour. After I wrote 'MBUNI' in St. Andrews during 1989, 'MBUNI' was developed and tested in the field during the initial few months of this research, and then used successfully to collect 7 months of focal data. A complete program listing and information on the structure of the program can be found in Appendix B, and the Users' Guide in Appendix C gives full details of how the program can be used.

'MBUNI' is menu driven and so is an easy tool to work with. It uses the principle of having key presses represent the occurrence of behaviours which have been defined by the user. The user creates a 'library' of behavioural categories which are to be associated with specified keys and makes certain descisions about how data are to be recorded. This 'library' is then consulted during the 'observation' part of the program, while the time and date are recorded automatically on the depression of the keys. Figure 2.6 is an example 'library' used during this research (and see below).

key	behaviour	s/d	prompt
,	rejection	1	
/	out_of_sight	1	
0	997.00	4	
1	999.99	4	
2	901.06	4	
3	101.06	4	
4	512.00	4	
5	600.13	4	
6	618.02	4	
7	105.13	4	
8	105.22	4	
9	616.01	4	
;	beyond_5m	3	
G	nipple_position	1	
Q	being_groomed	1	by whom?
R	receiv_affil_appr.	1	
U	male_in_conflict	1	which male?
W	supplanting	1	
Y	receiv_aggression	1	
a	resting	1	
b	attd_environ.	1	
c	social_expl	1	
d	expl_for_food	1	
f	feeding	1	on what?
g	on_nipple	1	
h	ventral_contact	3	
i	within_1m	2	which male?
j	other_contact	3	
k	within_arms'_reach	3	
l	arms'_reach_->_5m	3	
n	attd_social	1	
o	1_to_5m	2	which male?
p	no_male_within_5m	2	
q	grooming	1	whom?
r	make_affil_appr.	1	
s	moving	1	
t	avoid	1	
u	carried_by_male	1	which male?
v	vis_attd_(indist)	1	
w	supplanted	1	
x	environ_expl	1	
y	aggress	1	
z	active_expl	1	
#			
1	2 continuous		
2	3 continuous		
3	0 continuous		

Figure 2.6: Example 'library' used by 'MBUNI', showing the chosen keys (listed alphabetically) and the behavioural categories they represent, the subdivision (s/d) which the categories belong to, and the prompts which appear on the screen when some of the keys are pressed. For example, the key 'f' is associated with the behavioural category 'feeding', belongs to subdivision 1, and has a prompt for further information 'on what?'. This 'library' has three subdivisions to which the behavioural categories are allocated; the information at the end of the library shows that each subdivision uses continuous recording, and that s/d 1 'looks into' and records from s/d 2 and s/d 2 'looks into' s/d 3. Keys in the fourth subdivision are used as shorthand for food codes.

Data can be recorded continuously or by user-defined time sampling. Behavioural categories can be allocated to one of up to three subsections within the 'library' to facilitate the recording of simultaneously occurring behavioural states or independent aspects of the project. Different methods of data collection can be used for each subsection, and the data are stored in separate files. Figure 2.7 illustrates these features of data collection using 'MBUNI' in conjunction with the 'library' shown in Figure 2.6. A fourth subsection can be used to store frequently used codes or descriptions which the user associates with keys so that those keys can then be used as a shorthand e.g. food codes. For any key (except those used as shorthand codes), the user can stipulate that on the depression of that key, he is prompted for further information (e.g. if the behavioural category is 'grooming', then the user might want to be prompted to enter the information about who is involved, their IDs etc.) Additionally, there is the option to store in a single data file the behaviour recorded for a specified subsection and automatically whatever is also *currently* being recorded for another specified subsection i.e. to 'look into' another subsection and record both sets of data simultaneously in one data file. All this information is defined by the user and is stored in the 'library' along with the key associations. The 'library' can then be repeatedly loaded in for observation sessions on different occasions. Different 'libraries' can be created for different purposes and each used separately with the 'observation' part of 'MBUNI' for collecting different focal data.

At the start of an 'observation', the user names the files which the data will be stored in and the ID of the focal animal. Then pressing any key starts the focal session. During the focal, data are recorded by the depression of keys and entering any prompted information where required. Any prompts, prompted information and the behavioural category descriptions associated with the keys currently being recorded in each of the separate subdivisions are displayed on the screen, and updated as the entries are changed. Figure 2.8 illustrates the sequence of screen displays produced by the program during an observation session. The end of the focal is determined automatically when the appropriate time has expired (e.g. 30 minutes) and is signalled

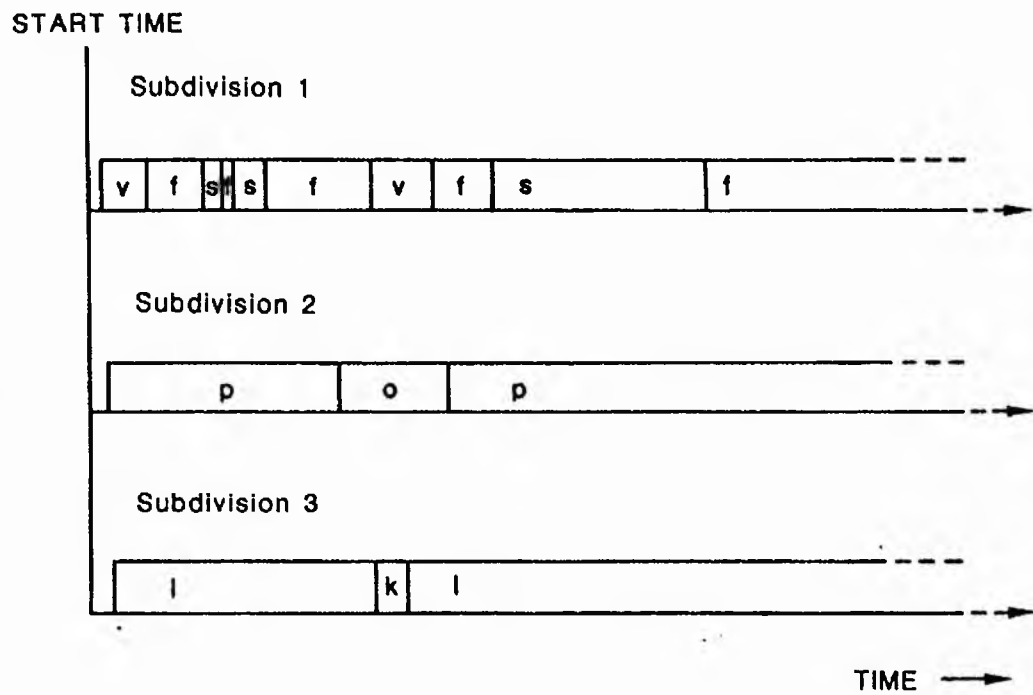


Figure 2.7: Continuous data collection using a 'library' which has three subsections.

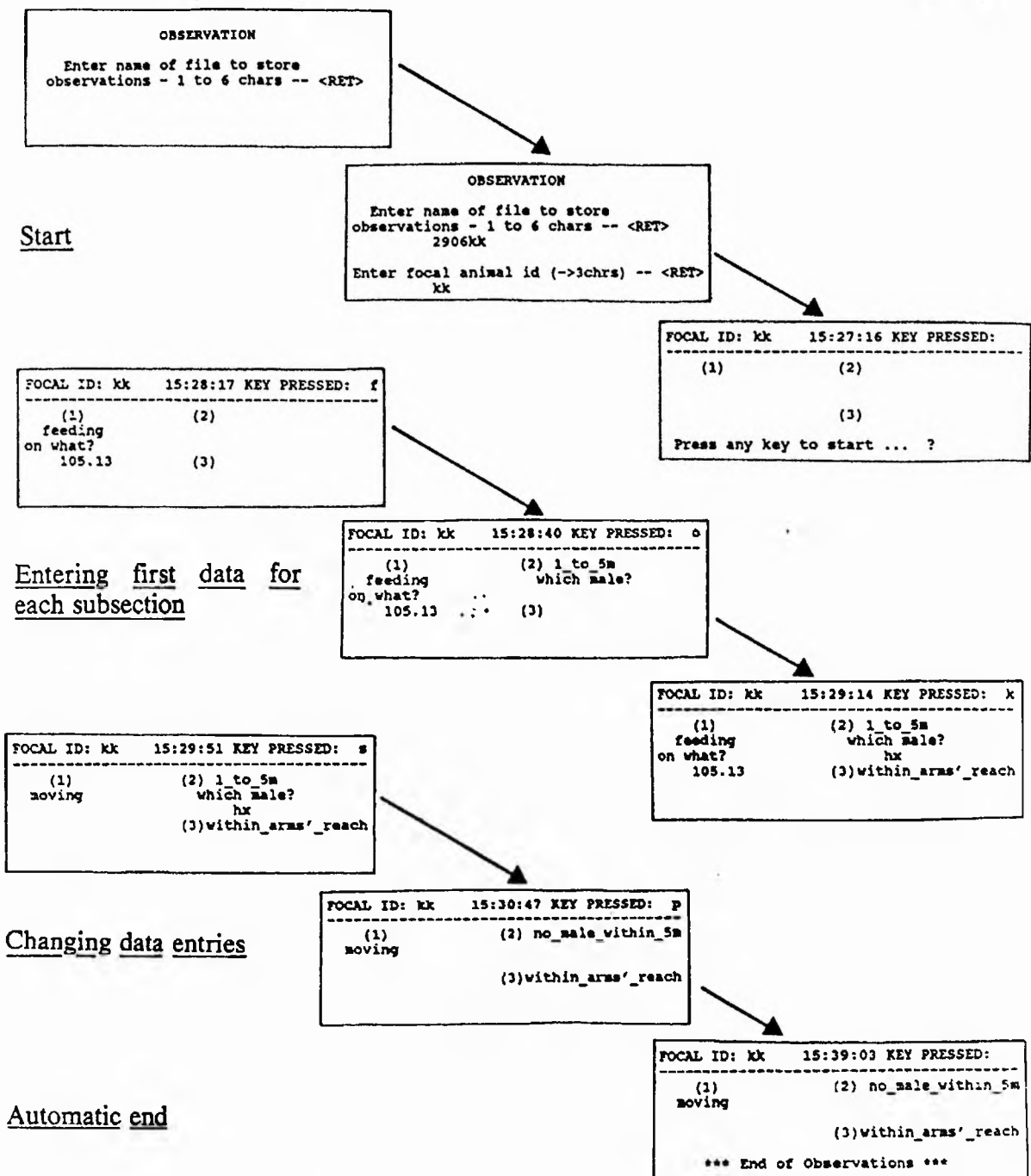


Figure 2.8: Example screen displays during the 'observation' part of 'MBUNI'.

by a double bleep from the computer.

Data are stored on disk in text files: each key press and any prompted information are stored rigorously in columns, with the time and date making each entry unique. This means the data can then be easily read directly into larger computers for analysis and manipulation, without the need for alteration. Figure 2.9 shows an example of data collected using 'MBUNI' with the 'library' shown in Figure 2.6. (See also Appendix C for full details of all the features of 'MBUNI'.)

Focal data collection and sampling:

All focal observations were made in 30-minute samples, using 'MBUNI' and a 'Portfolio' hand-held computer to record the data. Sticky labels for behavioural codes were stuck over the keys of the keyboard, and the computer was rested on an A4 size clipboard for stability (see Figure 2.10).

The activity of the focal animal, the proximity and identity of the nearest adult or sub-adult male if there was one within 5 metres, and the proximity of the focal animal to its mother were recorded continuously. (This enabled actual durations for the occurrence of each activity to be calculated during analyses of the data.) Table 2.4 (a) - (c) lists the mutually exclusive behavioural categories used for each of these aspects of the subjects' behaviour, in order of priority. The definitions of these categories are in Appendix A. (Analyses of the data on adult male proximity to subjects is not presented in this thesis.) These three aspects of behaviour were represented during data collection by separate subsections in the 'library' (activity budget: s/d 1; male proximity: s/d 2; mother contact: s/d 3): i.e. data on each could be collected independently yet simultaneously during the focal. (The 'library' used during this research is illustrated in Figure 2.6.) If 'feeding' was recorded, the species and part of the food eaten was entered as a code (e.g. 601.13 = *Sansevieria intermedia*.base (species.part)), and the number of bites of that food recorded using a counter key. If 'grooming', 'being groomed', 'carried by male' or 'with male in conflict' were recorded, the identity of the partner or male was entered in response to a prompt for further information. The

```

***          9:52:00 25:10:1990          {start time}
kk v -       9:52:01 25:10:1990 - -
kk f 101.06  9:52:12 25:10:1990 p -      2
kk s -       9:52:20 25:10:1990 p -
kk f 999.99  9:52:32 25:10:1990 p -      1
kk s -       9:52:34 25:10:1990 p -
kk f 556.99  9:52:41 25:10:1990 p -      1
kk v -       9:53:03 25:10:1990 p -
kk f 111.06  9:53:38 25:10:1990 p -      5
kk , -       9:54:05 25:10:1990 p -
kk s -       9:54:08 25:10:1990 p -
kk v -       9:54:10 25:10:1990 p -
kk s -       9:55:53 25:10:1990 p -
kk G -       9:55:54 25:10:1990 p -
kk s -       9:56:12 25:10:1990 p -
kk v -       9:56:14 25:10:1990 p -
kk s -       9:57:37 25:10:1990 p -
kk f 999.99  9:57:42 25:10:1990 p -      1
kk s -       9:57:45 25:10:1990 p -
kk v -       9:57:47 25:10:1990 p -
kk s -       9:59:01 25:10:1990 p -
kk f 999.99  9:59:07 25:10:1990 p -      1
kk s -       9:59:13 25:10:1990 p -
kk v -       9:59:16 25:10:1990 p -
kk s -       9:59:48 25:10:1990 p -
kk d -       9:59:50 25:10:1990 p -
kk g -       9:59:53 25:10:1990 p -
kk v -      10:00:18 25:10:1990 p -
kk s -      10:01:58 25:10:1990 p -
kk d -      10:02:04 25:10:1990 p -
kk f 901.06 10:02:05 25:10:1990 p -      1
kk f 999.99 10:02:17 25:10:1990 p -      1
kk f 101.06 10:02:21 25:10:1990 p -      1
kk s -      10:02:32 25:10:1990 p -
kk f 101.06 10:02:39 25:10:1990 p -      1
kk v -      10:02:43 25:10:1990 p -
kk s -      10:04:58 25:10:1990 p -
kk f 101.06 10:05:02 25:10:1990 p -      2
kk s -      10:05:07 25:10:1990 p -
kk f 903.06 10:05:16 25:10:1990 p -      2
kk f 902.06 10:05:45 25:10:1990 p -      1
kk s -      10:05:49 25:10:1990 p -
kk d -      10:06:34 25:10:1990 o hx
kk s -      10:06:37 25:10:1990 o hx
.. . .      . . . . .
.. . .      . . . . .
kk f 997.00 10:21:49 25:10:1990 p -      1
...          10:22:00 25:10:1990          {end time}

```

Figure 2.9: Extract from example of data collected using 'MBUNI'. Columns store the ID of the focal animal, the key pressed, the prompted information, the time and date, information from 'looking into' a specified other subdivision, and the number of bites of food eaten in a feeding bout. For example, the entry outlined records that subject kk feeds on *Cynodon* spp. grass blades at 10:02:05 on the 25th October 1990 and that 1 bite was eaten; simultaneously subdivision 2 is currently recording that no male is within 5m of the subject (p -).

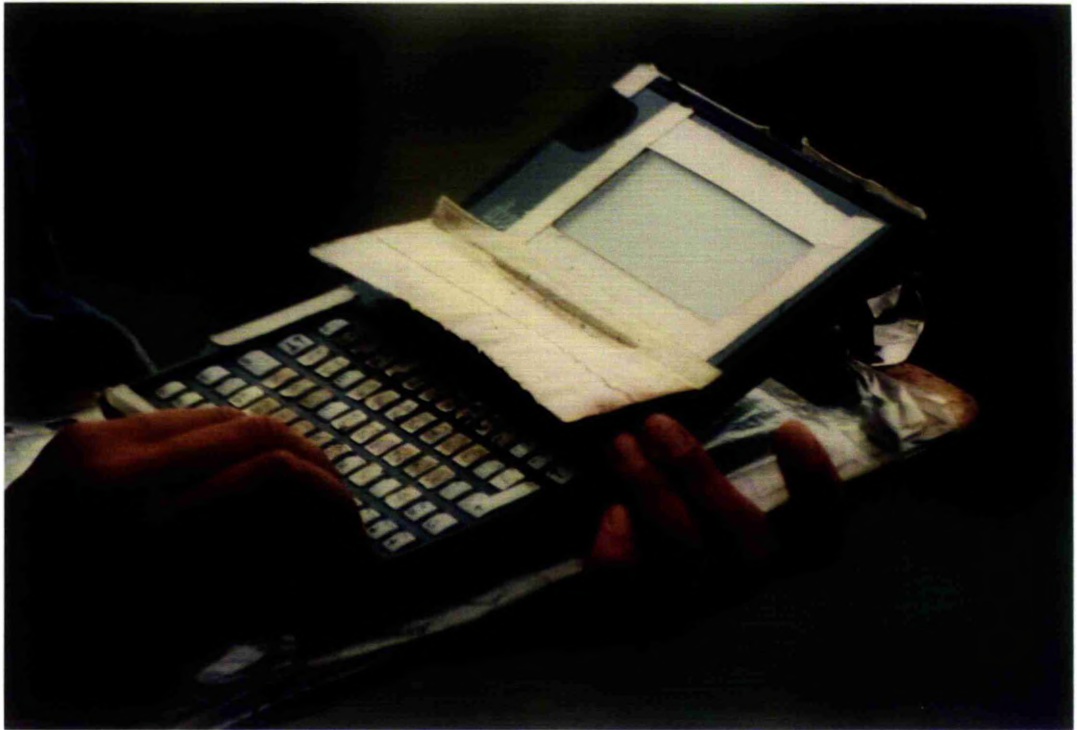


Figure 2.10: A 'Portfolio' hand-held computer being used to record focal data: labels were stuck on the keys to denote behavioural codes and the computer was rested on a clipboard for stability.

Table 2.4 (a): Activity budget behavioural categories, listed in order of priority; (b): Male proximity behavioural categories; (c): Mother contact behavioural categories. Each behavioural category is defined in Appendix A.

- (a):
- (1) FEEDING
 - (2) SUPPLANTING
BEING SUPPLANTED
 - (3) SUFFERING REJECTION
 - (4) INITIATING AFFILIATIVE APPROACH
RECEIVING AFFILIATIVE APPROACH
AVOIDING
INITIATING AGGRESSION
RECEIVING AGGRESSION
CARRIED BY MALE
WITH MALE IN CONFLICT
 - (5) IN NIPPLE POSITION
ON NIPPLE
 - (6) GROOMING
BEING GROOMED
 - (7) ATTENDING SOCIAL
ATTENDING ENVIRONMENTAL
 - (8) EXPLORING FOR FOOD
ENVIRONMENTAL EXPLORING
SOCIAL EXPLORING
ACTIVE EXPLORING
 - (9) VISUALLY ATTENDING
 - (10) MOVING
 - (11) RESTING
 - (12) OUT OF SIGHT

- (b):
- WITHIN 1m
 - 1m TO 5m
 - MORE THAN 5m

- (c):
- VENTRAL CONTACT
 - OTHER CONTACT
 - WITHIN ARMS' REACH
 - ARMS' REACH TO 5m
 - BEYOND 5m

category 'out of sight' was used immediately when a subject was not visible to the observer (for example in thick bush or when the observer had to cross a difficult gully) and this was automatically carried over to subdivisions 2 and 3 to maintain data validity. The 'library' was set up so that in the file for the activity budget data, information on the nearest male from subdivision 2 was also recorded (subsection 1 'looking into' subsection 2), and similarly in the file for male proximity, information on the subject's proximity to its mother from subdivision 3 was also recorded (subsection 2 'looking into' subsection 3). (These data were in fact not used in the analyses presented in this thesis.)

An example of the data collected during this research is that shown in Figure 2.9. Data files were stored automatically on memory cards placed in the disk drive of the 'Portfolio' during observations, and at the end of each day these were transferred to an Amstrad portable personal computer at camp and stored on 3¹/₂" magnetic disks. All analyses were then carried out in St. Andrews using the statistical package SPSSPC.

Following Barton (1989), five time-zones were used in order to balance the distribution of observations throughout the day: 0700-0915, 0915-1130, 1130-1345, 1345-1600, 1600-1815. A note was kept of which time-zone focal data were collected in for each individual through the month, and observations were thence spaced out so that an individual was not followed on successive days or in consecutive time-zones in the same week, wherever possible. Focal samples were taken of the behaviour of each subject in each time-zone at least once each month (except in October because of an injury preventing me from getting to the field). This meant that the subjects were not selected by rota within a month, but the biases of completely random selection were avoided in a practical way. Focals were repeated on an individual if they had been interrupted by the prolonged presence of a local person close to the observer, or if more than 15 minutes out of the total observation session were spent out of sight (e.g. if the focal subject was lost, or if the vegetation was too dense to continue).

Data reliability:

In April 1990, I had the opportunity to test the reliability of the behavioural categories I had chosen to use for focal data collection, during a supervisory visit by A. Whiten.

Having defined the behavioural categories and discussed them with Whiten, we then spent one day in the field checking the identification of the categories and carrying out time sample focal observations of subjects to measure the reliability of two observers using these categories. A subject was followed for periods of 8 minutes, during which the activity of the subject was recorded simultaneously yet independently every 15 seconds, on the bleep from a watch which was audible to us both. After an initial period of practice and discussion, 12 such focals were carried out resulting in 373 point sample observations.

The four most frequently occurring behavioural categories (feeding, moving, visually attending and environmental exploring) obtained over 80% reliability, and there was 100% reliability for recording unusual occurrences (e.g. being carried by male). Other behavioural categories (e.g. avoid, resting, receive affiliative approach) occurred too infrequently ($N = 1 - 10$ in 373 point samples) to be able to include them in the assessment of reliability.

Ranging data collection:

The program 'MBUNI' was also used to collect data on the location of the troop in the home range. Using a map of the study area which was divided into $1/4 \text{ km}^2$ squares, a 6-figure grid reference for the square which the centre of the troop was occupying was entered every hour, using the 'location' part of the program. (The 6-figure grid references used included '0' or '5' for the 3rd and 6th digits to denote anywhere in the $1/4 \text{ km}^2$ square, rather than a precise 6-figure grid reference.) After each entry, the grid reference was appended to the day's list, along with the time and date. The shortest distance between the new entry and the previous one was calculated by the computer and the cumulative distance travelled was recorded on disk with the

other data. The running total distance at the end of the day was therefore the length of the troop's day journey. The algorithm used for calculating the shortest distance between two 6-figure grid references used Pythagorus' theorem and is given in Appendix B.

Ad libitum data collection:

In addition to focal data collection, notes on the occurrence of predations by or on the baboons, intertroop interactions, consorts, copulations, grooming bouts, affiliative and aggressive behaviour, and the general behaviour and movements of the troop were made on an ad libitum basis. Records were also kept on the sleeping site at which the baboons were found in the morning and where they ended the day, and on the times of descent from the sleeping site, start of travelling, arrival at that night's sleeping site, and ascent to the sleeping site. More details on the method of ad libitum data collection can be found in the Project Manual in Appendix D.

Long-term demographic data collection:

Demographic records for STT were completed every month at the end of the month, based on daily census, female reproductive state and ad libitum data. Individual life history records were updated as appropriate. The data from the study year form part of the long-term records which have been maintained on this troop since 1986. The methodology for completing the long-term records is described in full in the manual in Appendix D.

Ecological monitoring:

At this site, ecological monitoring is carried out at the end of each month to provide information on plant phenology and productivity. This is part of the on-going long-term data collection, originally set up by Barton (1989). A number of techniques are used which involve measuring the total herb-layer green biomass, the baboon foods found in the herb layer and the baboon foods in trees and shrubs. Baboon foods are the

parts of plant species known to be eaten by baboons at this site i.e. those listed by Barton (1989) plus those few new foods observed eaten since Barton's study. Measures of baboon foods in the herb layer and in the trees and shrubs together comprise the baboon food biomass.

Data are collected at fixed sampling points ($N = 34$ until April 1990; 24 after April 1990) along 4 transects which are located in such a way as to provide a representative sample of habitat types within the baboons' home range (see overlay on Figure 2.2 for location of the transects).

Total herb layer green biomass is assessed using a pin-frame method, where 4 pins are randomly slotted down through a wooden frame and a count of the number of contacts between green and brown plant material and the pins is made.

The biomass of baboon foods in the herb-layer or loose on the ground is assessed by using a $1/4 \text{ m}^2$ portable wooden quadrat. The quadrat is placed on the ground at two permanent places at each sample point (Figure 2.11), and the number of items of each type of food are counted within the quadrat. So that the quadrat site is not disturbed, biomass is then calculated by multiplying these counts by the values of dry weight per item which have been obtained for each type of baboon food from sites away from the sample points. Samples of most known baboon foods have been collected by Barton and Whiten and phytochemical analysis carried out on them (Barton, 1989; Barton et al., in press).

Baboon food available from trees and shrubs is assessed by counting or estimating the number of food items present in 4 focal trees and 4 focal shrubs at each sample point. The biomass of baboon foods can then be calculated using dry weight values, and multiplying the results by the density of such tree and shrub species within the home range.

Full details of the techniques used can be found in the Project manual in Appendix D.

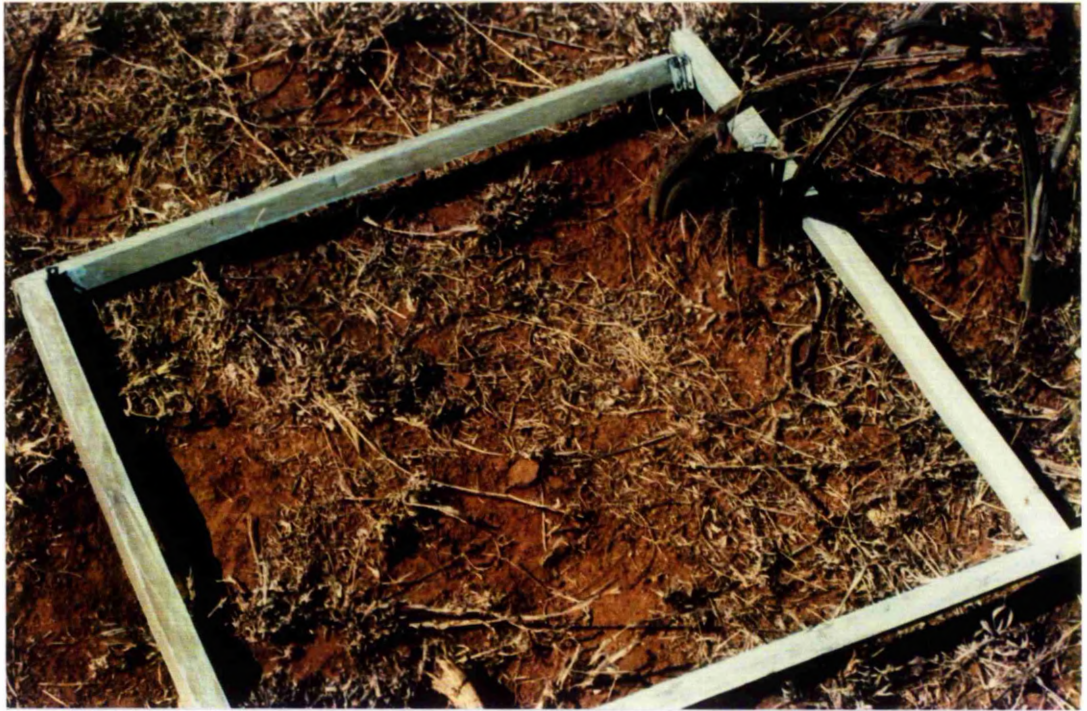


Figure 2.11: The 0.25m^2 quadrat used to assess the biomass of baboon food in the herb layer: the number of items of each food type are counted within the quadrat.

CHAPTER 3: LONG-TERM AND SEASONAL VARIATION IN RAINFALL AND FOOD AVAILABILITY

INTRODUCTION

Palaeoclimatic research based on pollen and sedimentary analyses has demonstrated cyclical fluctuations in the palaeoenvironment of the earth (Foley, 1987). Such climatic and environmental changes prevail up to the present day: the examination of patterns of climatic change over centuries has shown an association with sunspot cycles, providing evidence for natural cycles of various lengths e.g. 5 - 7 years; 170 - 200 years (Pearson, 1978). Similarly, Wood and Lovett (1974) have shown that an 11 year cycle has a great influence on the rainfall/drought pattern at Addis Ababa, Ethiopia, which is within the range of present day baboons (*P. hamadryas*).

At Amboseli National Park, Kenya, where savannah baboons are found, there is evidence of cyclical changes in the pattern of rainfall (Western and Van Praet, 1973). Historical evidence indicates that in the 19th Century, the environment at Amboseli experienced heavy rainfall resulting in a swampy habitat with few trees. After 1890, Amboseli experienced less rainfall and became drier. However, since 1960 there has been an increase in rainfall, which according to Western and Van Praet (1973), resulted in a 4m elevation in the water table. This has introduced a high level of soluble salts into the rooting layer, resulting in drastic changes in the ecology of the Park: for example, an inhibition of water uptake in the Park's Fever trees (*Acacia xanthophloea*) causing their death, and the change of plant communities to those which flourish in saline conditions. In this part of Kenya therefore, there appears to be a cycle of about 80 years, currently returning conditions to the more swampy environment experienced in the previous century after an intermediate period of dryness.

In addition to such long-term climatic cycles which affect vegetation and resources, environments may experience annual seasonal cycles which affect the temporal distribution of resources within the year, and the nature of the local habitat.

Savannah environments in particular show marked seasonality, in contrast with forest environments where rainfall is distributed more continuously throughout the year (Richard, 1985; and see discussion in Chapter 1)¹. For example, there is seasonal variation in the distribution of rainfall throughout a year recorded at Gilgil (Harding, 1976): typical of savannah rainfall patterns, for 8 months of the year rainfall was below the monthly average for that year, and most of the rainfall occurred in two periods (rainy seasons). At Amboseli, data on the monthly distribution of rainfall show that in some months of a year there may be no rainfall (Altmann, 1980; Post, 1982).

Long-term data from Mikumi in Tanzania (yellow baboons) show the recurring cyclical nature of the occurrence of rainfall over a period of 20 years (Norton et al., 1987). The distribution of rainfall at Mikumi occurs over one rainy season, in contrast with the two experienced at most sites in central Africa. But also there is marked yearly variation in rainfall patterns (Norton et al., 1987). Data on the annual rainfall at Gilgil (1971 - 1980: Strum and Western, 1982) similarly indicate large yearly differences, with values ranging from 472mm (1976) to 791mm (1977). Considerable variation in the amount and distribution of rainfall from year to year is characteristic of savannah environments (Foley, 1987).

Biomass and primary productivity of vegetation tend to decrease with declining moisture (Richard, 1985), and annual rainfall has been shown to be a reliable index of plant biomass and primary production (Coe et al., 1976; Dunbar, 1990, in press). The relationship between rainfall and plant biomass means that the patterns of rainfall experienced in savannah environments cause a highly seasonal pattern of plant production. Plant cycles are synchronised with seasonal rainfall cycles: after the rains, there is new leaf growth and grasses produce new shoots and stems. As the dry season progresses this growth slows down, the grass turns brown and protein content falls (Foley, 1987). Generally, most species of tropical plant produce flowers and fruits in

¹ Forest environments can experience a short dry season, e.g. 3 months at Lope, Gabon (Tutin et al, 1991), but the effect is not as marked as in savannah environments: there are always some species of tree fruiting during each month of the year (Tutin et al., 1991).

the wet season (Hladik, 1977; Peters, O'Brien and Box, 1984), though some species react to prolonged drought by producing seeds and fruit, making them abundant in the extreme dry season (Foley, 1987). The association of plant production with rainfall patterns and the limited periods of fruit and flower production in savannah environments contrast with the presence of leaves, flowers and fruits during much of the year in tropical rain forest environments, where a more continuous pattern of rainfall means little synchrony in production (Richard, 1985) (e.g. see Tutin et al. (1991) for forest food availability).

Researchers have recognised that in order to understand the behaviour of primates it is important to relate behaviour to local resources, and in recent years the emphasis of field studies has shifted to consider this ecological viewpoint (Chivers and Hladik, 1978). Measures of annual rainfall and estimations of biomass give some indication of environmental conditions (e.g. Strum and Western, 1982), and Dunbar (in press) has examined the influence that a variety of environmental factors have on activity budgets, but most pertinent is information on the availability of actual food resources (those species actually eaten as opposed to total biomass values), particularly measures of the amount and distribution of the food species and their nutritional values. Without such data, the assumption that the wet season means abundant food resources and that the dry season means scarce food resources remains untested (Barton, 1989).

Several studies have involved the examination of food availability: for example, Peters, O'Brien and Box (1984) carried out a comprehensive survey of the seasonal availability of wild-plant foods in East and South Africa focusing on human foods. They present data on the number of species which provide types of food and the seasonal occurrence of these foods. Gatinot (1978) mentions with reference to the diet of the West African red colobus that some of the flora exhibited seasonal cycles of leaf, flower and fruit production, though he does not specifically present data on this. In his study of the dispersion of Malaysian forest primates, Aldrich-Blake (1978) used 7 hectare plots, and recorded the presence of young leaves, shoots, flowers and fruits on trees whose trunks were greater than 50cm in circumference, to indicate spatial and

temporal differences in potential food availability. In their on-going project at Lope in Gabon, Tutin et al. (1991) collect monthly phenological data on leaf, flower and fruit production on 10 individuals of 60 tree species whose fruit is important in the diet of chimpanzees and gorillas. In her study of vervet monkeys at Amboseli, Lee (1981) measured the density of 8 major plant food species by censusing quadrats in the monkeys' home range and in conjunction with values for canopy availability, this was used to calculate food availability. However, Wrangham (1977) attempted no strictly independent measures of food availability when studying the feeding behaviour of chimpanzees at Gombe. He controlled for change in the environmental factors that might affect behaviour by comparing behavioural observations from the same months in successive years, and assumed that the major difference was therefore in food availability.

Primate studies which record absolute food availability are, however, rare (Barton, 1989). With reference to baboon studies specifically, at Mikumi, food availability was estimated by walking through and scanning the environment in the troop's home range for presence of foods when they were being eaten by the baboons, and a transect survey where the condition of vegetation was assessed quantitatively corroborated these data (Norton et al., 1987) but absolute food availability was not measured. At Amboseli, Post found quantitative assessment of seasonal fluctuations in total amount of baboon food available too difficult to carry out (Post, 1981), and so used indications of relative availability in his analyses. For 8 food items (for which at least 10 individuals were sampled each month), he plotted the proportion of plants containing that food item in medium or heavy abundance. While it was impossible from these data to examine the total amount of food availability, the abundance of any single food could be compared in different months (Post, 1982). However, Post notes that 'unless the nature of seasonal variability in food availability is understood, the presence or absence of variability in the proportion of time spent in different activity states may be difficult to interpret' (1981: p370). The only known studies of baboons where overall food availability has been measured are Byrne, Whiten and Henzi's study

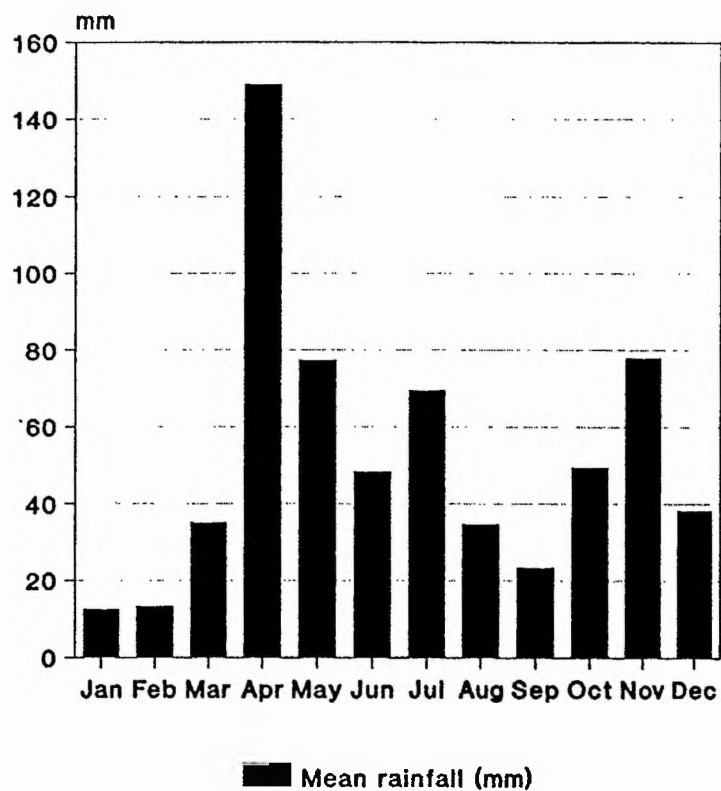
of chacma baboons in the Drakensberg Mountains (Byrne et al., 1990) and the work at Chololo (Barton, 1989; Barton et al., 1992, in press). The present study involved the continuation of data collection on absolute food availability initiated by Barton et al., and is also able to report on the results of this work over a period of five years since 1986.

In the following sections I present long-term data on variations in rainfall, biomass and food availability at Chololo to demonstrate the occurrence of seasonal fluctuations. I examine the relationship between these variables, and present data on the seasonal distribution of component food types which made up the diet of the baboons, especially the food resources provided by *Acacia* trees. Data on fluctuations in these aspects of the environment provide a context in which to interpret the behaviour of the study troop as a whole (Chapter 4) and of individuals in the troop (Chapter 7).

VARIATION IN RAINFALL

The mean annual rainfall at Chololo from 1986 to 1990 was 628.7mm. The mean monthly rainfall from 1986 to 1990 is presented in Figure 3.1. The general distribution of rainfall throughout the year falls broadly into two periods, peaking in May and November, with drier periods of little rainfall in between.

However, the general rainfall pattern described by these mean values conceals the yearly variation experienced by baboons in the amount of rainfall and its distribution throughout the year. The monthly rainfall at Chololo from January 1986 to December 1990 is presented in Figure 3.2, and Table 3.1 presents the values for annual rainfall for each of the years. 1987 experienced only half the mean annual value of rainfall (315.2mm). This low value was due to low monthly values but also the complete absence of rain for 4 months in the year (see Figure 3.2). A period of no rain from September 1987 to February 1988 (excepting the less than average rainfall in the month of November - normally the second peak of rainfall) effected a period of near-



Collected at Geoffry's House, Chololo

Figure 3.1: Mean monthly distribution of rainfall (1986 - 1990).

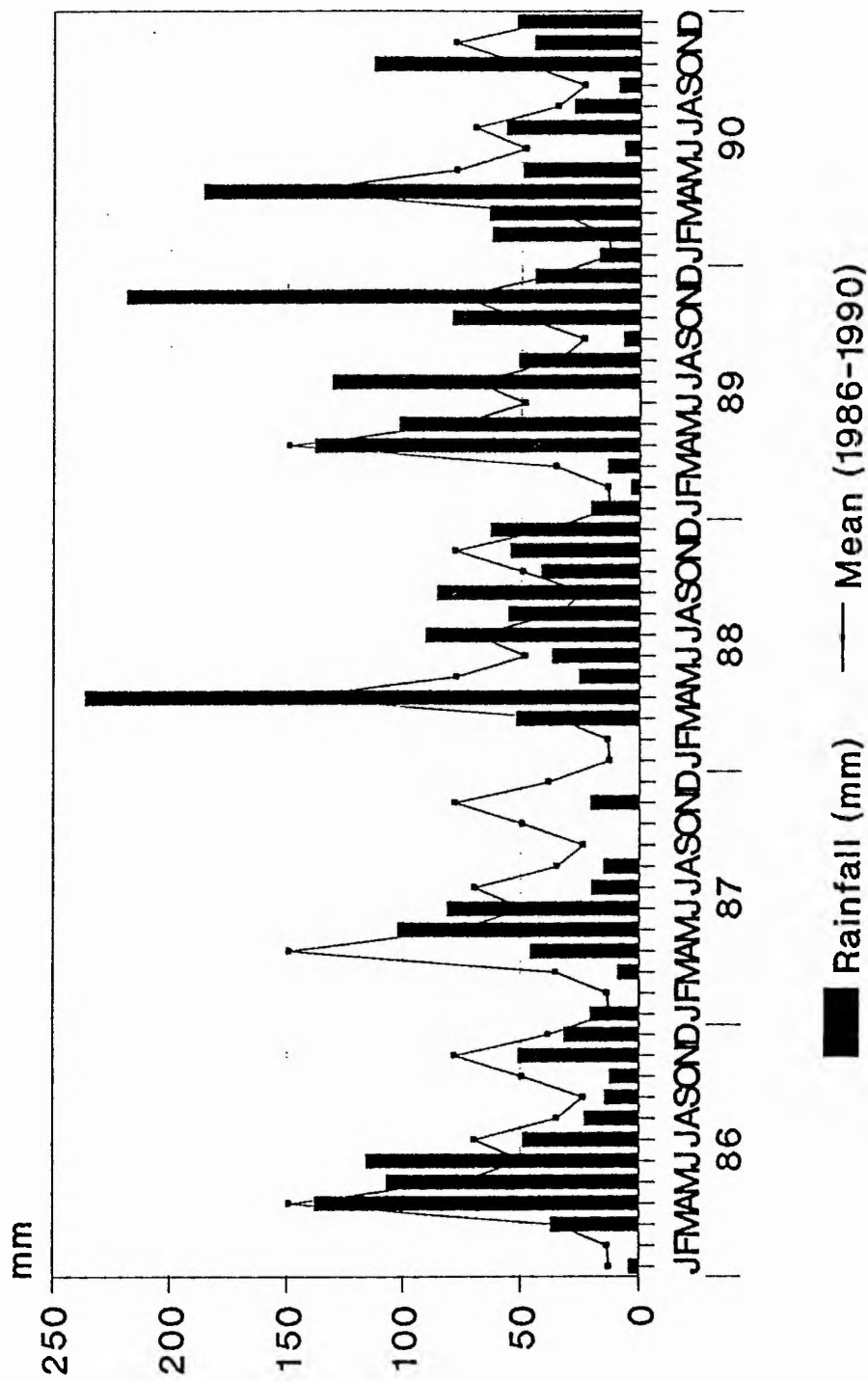


Figure 3.2: Monthly rainfall from January 1986 to December 1990. The mean monthly rainfall over five years (1986 - 1990) is presented repeatedly for each year.

Table 3.1: Annual rainfall from 1986 to 1990; values of Pearson's correlation coefficient (R) for monthly rainfall and number of rain days correlated between consecutive years. (N = 12)

		R	
TOTAL ANNUAL RAINFALL (mm)		MONTHLY RAINFALL	MONTHLY NUMBER OF RAIN DAYS
1986	584.8	0.824 **	0.682 **
1987	315.2	0.055	0.416
1988	741.8	0.415	0.537 *
1989	811.2	0.420	0.560 *
1990	690.4		
$\bar{x} = 628.7$		** p < 0.01	* p < 0.05

drought conditions. Conversely, the high amount of rainfall experienced in 1989 was mainly due to the very high rainfall in November of that year.

The irregularities in the amount and timing of rainfall across years is emphasised in Figure 3.3 where the annual monthly rainfall distribution for each of the five years are presented vertically above each other. In four out of five of the years, the amount of rainfall in the first rainy period peaked in April, but in 1987, the peak occurred later, in May. In most years, a second peak of rainfall occurred in November. This was large in 1989, but not evident in 1988, and occurred earlier in 1990, in October. In some years there was additionally a slight peak in rainfall in July (especially noticeable in 1989).

The predictability of the pattern of rainfall was examined by correlating the monthly rainfall values and the number of days of rain in each month between adjacent years. In addition to the amount of rainfall, the number of rain days was used as an index of the distribution of rainfall throughout the year and similar correlations performed. The resulting values of Pearson's correlation coefficient (R) are presented in Table 3.1. There is a strong correlation between the monthly rainfall distribution of 1986 and 1987 ($R = 0.824$, $p < 0.01$), but there are no other significant correlations between the monthly rainfall of consecutive years. There is a significant correlation between the number of days of rain per month in 1986 and those in 1987 ($R = 0.682$, $p < 0.01$), and a weaker though still significant correlation between the monthly rain days in 1988 and 1989, and between 1989 and 1990. Using either index of monthly rain distribution, the correlation between the rainfall patterns in 1987 and 1988 is poor (rainfall: $R = 0.055$; rain days: $R = 0.416$).

The predictability of annual rainfall patterns from those of the previous year is good for 1986/1987, but poor for the years 1987 - 1990. Predictability of the number of days of rain per month from those in the previous year is better than the amount of rainfall, but not very reliable. Overall, predictability of rainfall patterns is poor between consecutive years. However, there are significant correlations between the patterns of rainfall from 1986 and those from 1988 (rainfall: $R = 0.560$, $p < 0.05$;

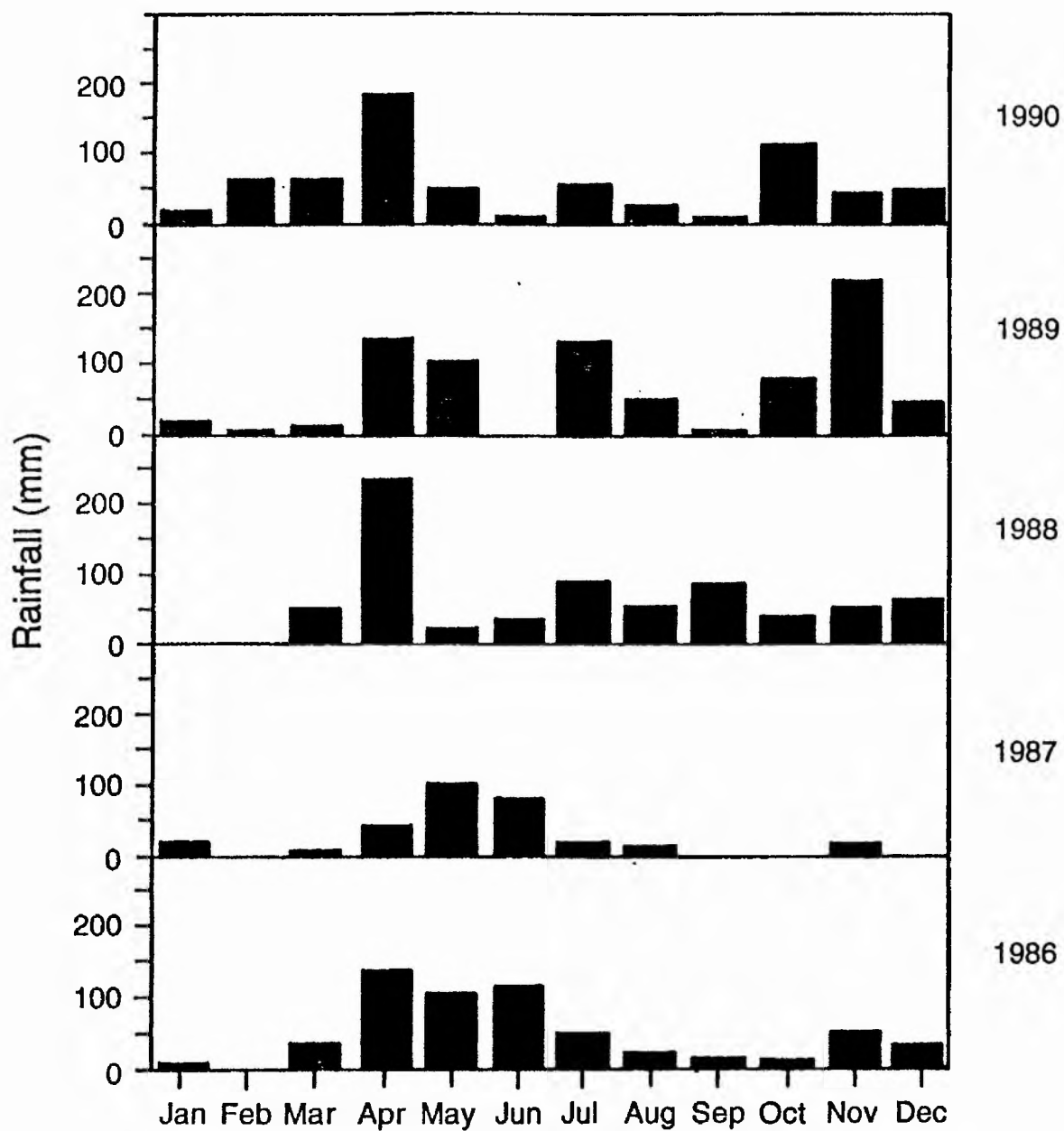


Figure 3.3: Monthly rainfall from January 1986 to December 1990 presented separately by year.

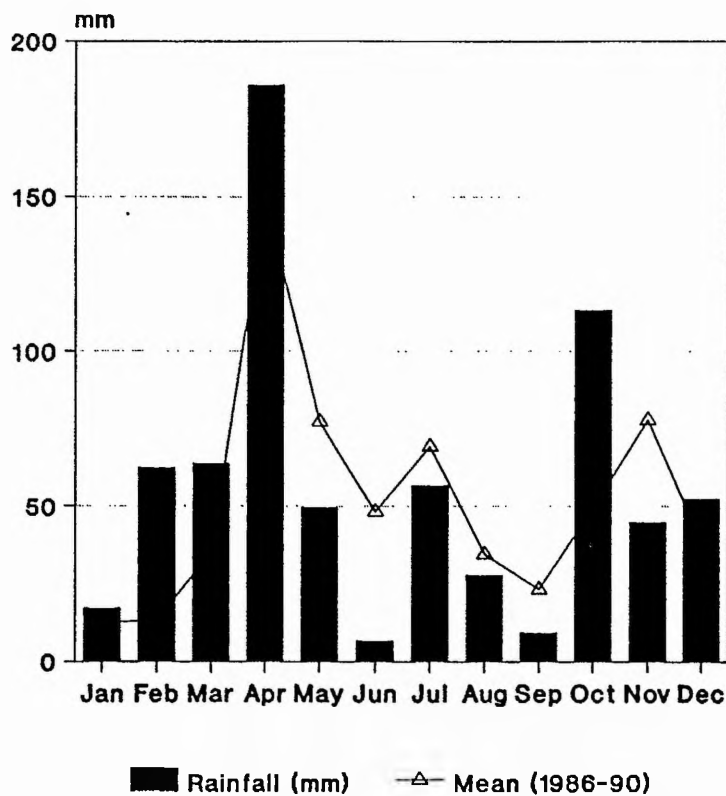
rain days: $R = 0.616$, $p < 0.05$), and between the amount of monthly rainfall in 1988 and 1990 ($R = 0.709$, $p < 0.01$), which indicate a certain amount of predictability in rainfall patterns in alternate years². Variability in rainfall patterns between years is high, but these correlations are all positive and thus indicate that the general seasonal cycle of rainfall is pervasive, even if in some years the distribution of rainfall deviates from it quite substantially.

The high variability in rainfall patterns at this site from year to year is reinforced by data from the nearby settlement of Dol Dol (acquired by Dr Strum) which show a similar variability in the amount and timing of rainfall over a period of 18 years.

The data presented here from Cholulu demonstrate that at this site there is generally a biannual cycle of rainfall where the amount of rainfall varies seasonally throughout the year, but that the pattern is not predictably regular: in some years there are long periods of no rain, and in other years there are months of high rainfall in months which are usually dry. Such variability is consistent with that found at other savannah sites. Data from consecutive years at Amboseli (1974-1976: Post, 1982; Altmann, 1980) demonstrate differences in the pattern of monthly rainfall, and as mentioned earlier, the long-term data from Mikumi illustrate yearly variation in rainfall distribution. Long-term field projects which include data collection on environmental factors such as the data presented here, enable us to recognise the cyclical nature of fluctuations in rainfall, but they also illustrate the variability in patterns of rainfall. These inter- and intra-annual variations make it difficult to delimit traditional 'wet' and 'dry' seasons in every year, and inappropriate to categorise an environment based on a single year's annual rainfall values.

For example, the amount of rainfall during the study year (1990) was higher than average for the first 4 months of the year and again in October, but less than the mean value during the rest of the year (Figure 3.4). The rainfall in July and the early occurrence of a high peak of rainfall in October was also 'non-typical', and the total

² An autocorrelation over all years would also elucidate inter-year predictability.



Collected at Geoffry's House, Chololo

Figure 3.4: Monthly distribution of rainfall in 1990, and the mean monthly rainfall over five years (1986 - 1990).

annual rainfall for 1990 was higher than the mean value over the five years 1986 to 1990.

As well as temporal variation in rainfall, it is important to recognise the existence of spatial variation in rainfall distribution. It was my subjective impression that rainfall was greater in the western part of the home range (Chololo) than in the eastern part (the Reserve), but the data on rainfall presented here were collected at only one point within the home range of the baboons (Geoffrey's House, Chololo), so analysis of this aspect of rainfall patterns has not been possible. Rainfall data are presently being collected at six other points within the baboons' home range (by workers at a Kenyan government climatic station and U.N.B.P., at sites on the Reserve). These data were not available to me at the time of writing this thesis, but their analysis in the future will be a valuable addition to the long-term environmental records of the research at this site.

VARIATION IN BIOMASS

Data on two types of biomass are collected at this site: estimates of green herb layer vegetation (GREEN BIOMASS) and estimates of foods known to be eaten by baboons (BABOON FOOD BIOMASS) (see Chapter 2 and Appendix D for methods of data collection). Green biomass values are available from August 1986 - December 1990, and analyses of these data are presented here. However, presentation of data on baboon food biomass is limited in this thesis to the results from 1990.

Baboons at Chololo have been observed to feed on 1 - 4 parts of 89 plant species (see Barton, 1989, for Chololo complete food list, and Appendix F for the top ten foods eaten by subjects during this study). The major staple foods of these baboons are generally found in the herb layer (blades, flowers and corms/bases of grasses and leaves, flowers and fruits of herbs), but the reproductive parts of *Acacia* trees, and the leaves, flowers and fruits of various shrubs also make up a substantial part of their diet. These baboons also eat succulent plant species, particularly the bases of *Sansevieria*

intermedia and the pads of *Euphorbia nyikae*. (The diet of young baboons during 1990 and seasonal variations in their diet are discussed in Chapter 7.) Measures of the presence of all these food types are included in the calculation of baboon food biomass values. (Patterns of food availability from *Acacia* trees and their relationship to rainfall are discussed specifically in the next section.)

Figure 3.5 presents data on green biomass and baboon food biomass values during 1990. Both measures of biomass show fluctuations in their values throughout the year.

There is clearly a strong relationship between the values of green biomass and the pattern of rainfall. Indeed, there is a very strong correlation between green biomass and rainfall in the same month ($R = 0.888$, $p < 0.001$). However, the effect of rainfall is likely to be cumulative (Barton, 1989). Correlating green biomass with rainfall in the same plus the previous month and previous two months gives strong positive correlations, presented in Table 3.2, which support this hypothesis. Using the data from 1986 - 1990, correlating values of green biomass with rainfall in the same and cumulated previous months results in similar strong positive values (Table 3.2). The strongest correlation was with cumulative rainfall in the same plus previous month ($R = 0.737$, $p < 0.001$), which is consistent with the cumulative relationship between vegetation in the herb layer and rainfall.

The influence of rainfall on plants in the herb layer is also apparent in an examination of annual variation in the quality of the plant items present. The 'greenness' of the existing plant material was assessed on a scale of 0 - 4 during herb layer ecological monitoring (see '% Green' in Appendix D). Figure 3.6 presents the monthly mean data for 1990 over all plots. The estimates of 'greenness' clearly fluctuate throughout the year, in relation to rainfall as described in the introduction (Foley, 1987). In the period June - September, the quality of the plant material that was present was low, compared with that during April and November (the rainy periods). The extreme effect of rain on herb layer vegetation is illustrated in Figures 3.7(a) and 3.7(b) (photographs taken at the same place after a period of rain and during

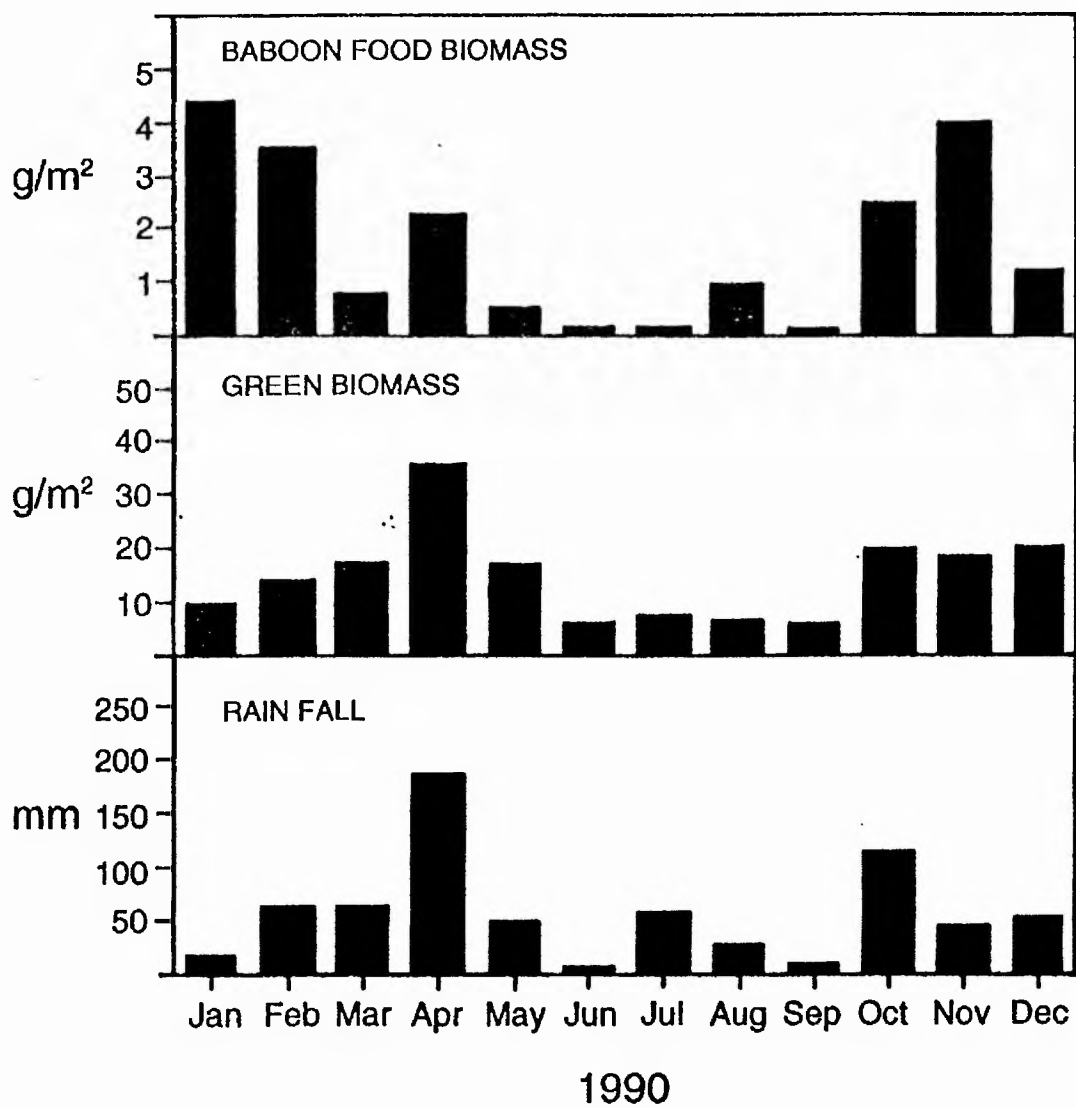


Figure 3.5: Monthly distribution of rainfall, green biomass and baboon food biomass in 1990.

Table 3.2: Values for Pearson's correlation coefficient for green biomass in 1990, green biomass from 1986 to 1990, and baboon food biomass in 1990, correlated with rainfall in the same month, in the same plus previous month, and in the same plus previous 2 months. [Sample size in square brackets]

	RAINFALL IN SAME MONTH	CUMULATIVE RAINFALL (SAME + PREV)	CUMULATIVE RAINFALL (SAME + 2 PREV)
GREEN BIOMASS (1990) [12]	0.888 ***	0.811 ***	0.503 *
GREEN BIOMASS (1986 - 1990) [39]	0.673 ***	0.737 ***	0.589 ***
BABOON FOOD BIOMASS (1990) [12]	0.204	0.124	0.204

*** p < 0.001

* p < 0.05

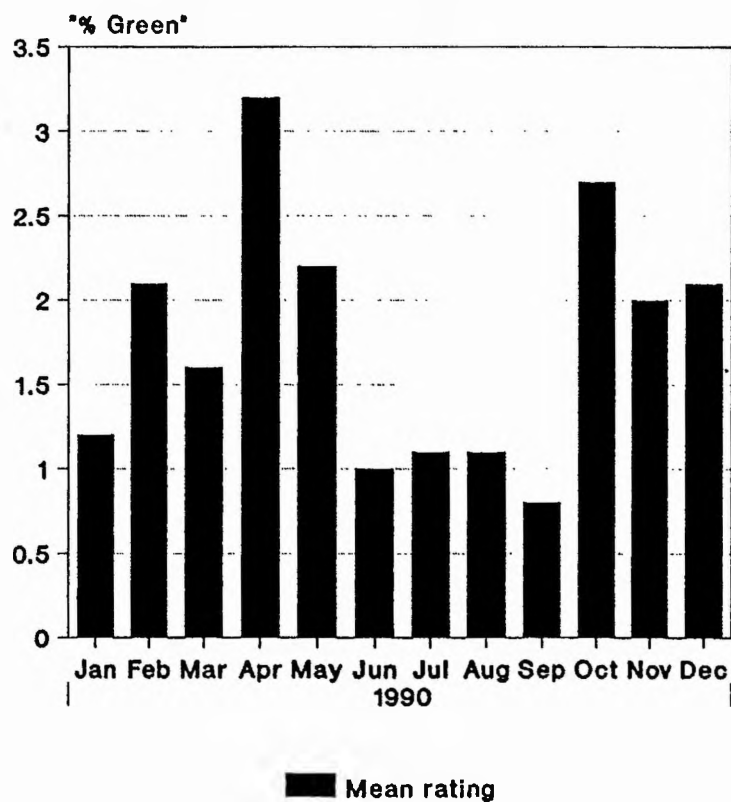


Figure 3.6: Monthly distribution of mean "% Green" ratings in 1990: "greenness" of plant material in 0.25m² quadrats, assessed on a scale of 0 - 4 relating to percentage (see Appendix D for method).



Figure 3.7(a): Fever Tree Gully after a period of rain: new growth in the herb layer follows rainfall.



Figure 3.7(b): Fever Tree Gully during the long dry season: no new growth in the herb layer; existing plants turn brown and die back.

the long dry season).

However, examining baboon food biomass in 1990, although there were seasonal fluctuations in the values, there was no such clear relationship with rainfall. The correlations between total baboon food biomass and rainfall in the same and cumulated previous months were poor (see Table 3.2) and not significant. These data from 1990 contrast with those of Barton (1989) who found that for data from 8 months in 1986, baboon food biomass followed the same pattern of decline in the dry season as that of green biomass over the same period. In contrast with the data presented here, he found good correlations between baboon food biomass and cumulative rainfall. The correlations between the herb layer component of total baboon food biomass and rainfall for 1990, however, are positive though not significant (rainfall in the same month: $R = 0.452$, $p = 0.140$; rainfall in same + previous month: $R = 0.438$, $p = 0.155$), adding some support to the evidence that herb layer biomass and the biomass of baboon foods in the herb layer are influenced by rainfall patterns. Total baboon food biomass is not influenced by rainfall in this way because of the additional component of biomass contributed by the trees and shrubs.

Figure 3.8 presents the monthly total baboon food biomass estimates divided into the main components of types of baboon food. Some foods are present throughout the year, for example, *Sansevieria intermedia* and *Euphorbia nyikae*. (Following Barton (1989), corms were only included in the calculations of biomass for the months where they were observed being eaten i.e. January and February in 1990). Food resources in the herb layer (particularly grass and herb leaves) dominate the estimates of baboon food biomass and, as already noted, show a pattern of fluctuations in response to rainfall. *Acacia* and shrub leaves are also prevalent at times of heavy rainfall. However, the reproductive parts of *Acacia* trees, particularly pods, are a substantial component of biomass and vary in their availability, with pods being present at highest levels during the early part of the year. This helps to explain the differences between the results in this study and those of Barton (1989): Barton's data from May - December did not include the peaks of pod production that usually occur early in the

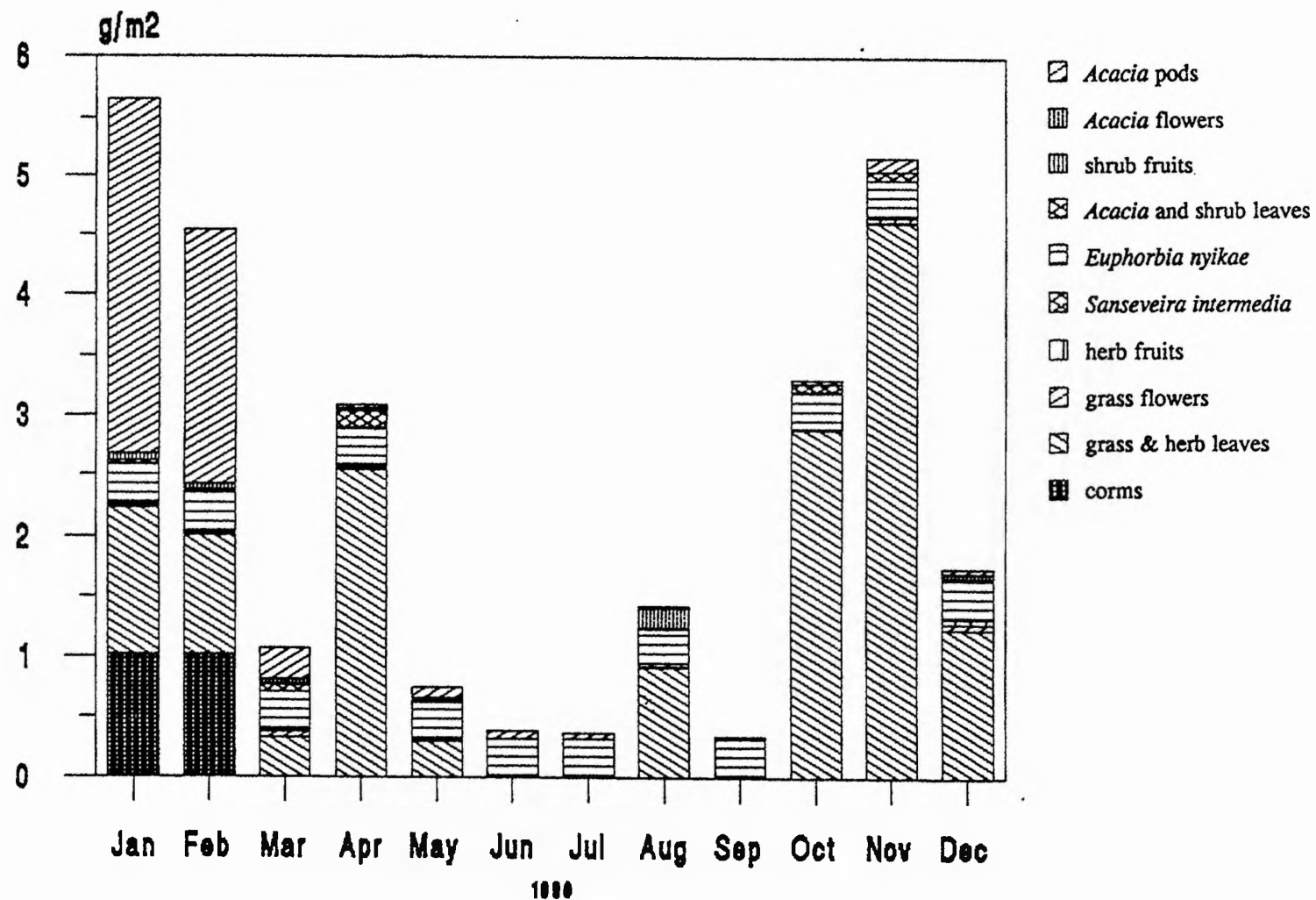


Figure 3.8: The composition of baboon food biomass in 1990, presented by month.

year (see *Acacia* data in the next section) so the relationship between baboon food biomass and green herb layer biomass would be expected to have been closer in his analyses. The biomass of baboon foods in the trees and shrubs make a significant contribution to the estimates of total baboon food biomass on top of the biomass of those foods found in the herb layer, and the timing of their availability may be particularly important to the baboons. The occurrence of *Acacia* flowers in August 1990 was likely to have been an important dry season food resource given there were very few resources available in the herb layer in June - September, although in this year there were also some grass and herb leaves produced in response to rainfall in July.

Barton (1989) found a very high correlation between green biomass data and baboon food biomass data for the 5 months for which both were collected at the same plots ($R = 0.97$, $p = 0.003$, $N = 6$). When the data from the same plots are examined for 1990, there is a similarly significant correlation between green and baboon food biomass ($R = 0.81$, $p < 0.001$, $N = 8$). However, the correlations between green biomass values and those of baboon food biomass calculated from data from all sampled plots on the transects (as presented in Figure 3.8) are poor ($R = 0.30$, N. S., No. of plots where baboon food biomass was recorded = 34 (Jan. - Mar.); 25 (Apr. - May; 24 (Jun. - Dec.)). Better, though not significant, correlations with data from all the sampled plots are obtained when using just the biomass of baboon food in the herb layer (i.e. not including that found in the trees and shrubs) ($R = 0.60$). So while data from the pin-frame technique used to estimate green biomass can also be generalised to the biomass of baboon foods in the herb layer throughout the home range area, they cannot be used to accurately estimate total baboon food biomass throughout the home range.

There are clearly seasonal fluctuations in the biomass of baboon foods available throughout the year. Measures of total baboon food biomass generate a more accurate and detailed picture of what may affect the baboons' behaviour. The distinction of 'wet' and 'dry' seasons is useful when discussing the biomass of the herb layer, because of the influence rainfall has been shown to have on growth and production, but such a simplistic distinction is not appropriate when referring to baboon food biomass because

of the phenology of the different food species and the associated complexity of their patterns of availability. (Analysis of the baboon food biomass data from 1986 - 1990 will provide valuable insights into this complexity, but this has not been possible in this thesis.) With respect to these data on actual baboon food biomass, however, I suggest it is more meaningful to make the distinction between periods of resource abundance and resource scarcity than to contrast 'wet' and 'dry' seasons. In 1990, there was a period of food scarcity in June - September, which coincided with the long dry season. October - December, during the short rains, was a period of abundance where high biomass values were mainly comprised of food in the herb layer. However, in January and February, the short dry season, there was also abundant food, though this time in part comprised of pods.

Byrne et al. (1990) distinguished between the availability of 'easy-to-get' and 'hard-to-get' foods when examining their baboon food biomass data. They considered that 'hard-to-get' foods, such as corms, were actually available all year round though they may not have been chosen for eating when there were 'easy-to-get' foods available and that it was the availability of the latter type of food which showed a pattern of seasonal fluctuations which was compatible with the observed diet of the baboons. No such distinction between food types has been made in this study. However, the results presented by Byrne et al. emphasise the importance of examining in detail the availability of component parts of these biomass estimates when studying the behaviour of an eclectic omnivorous species.

Finally, it is worth reiterating that these data on the biomass of baboon food are only estimates of absolute food available in the baboons' home range. In the ecological monitoring used at this site (see Appendix D), there are some problems in assessing underground items (e.g. corms and *Sansevieria intermedia* bases (see Barton (1989)) and whether the location of the transects means that they truly represent the habitat in the home range. Sampling more frequently than once a month would ensure that the occurrence of some food resources (e.g. *A. nilotica* pods) was more accurately represented; however, the techniques employed do provide detailed data on actual

biomass and food availability from which to make these estimates.

Strum and Western (1982) showed that indices of food abundance specifically incorporating the competition for food from ungulate competitors predicted fecundity in female baboons. Since March 1990, large mammal counts have been carried out in the home range of the baboons. These data show that the biomass of herbivores within the baboons' home range varied across the year. While the values of biomass presented here do not directly include any measure of the effect of other animals on the biomass of food available to the baboons, they are based on the biomass which remains, therefore already incorporating this factor.

Spatial variation in availability is another important aspect of baboon food biomass analyses, especially with respect to the ranging behaviour of the troop (see Chapter 4). The data presented here represent the whole home range of the baboons. It would be interesting to analyse separately the data for Chololo and the Reserve and to examine patterns in the spatial distribution of plant resources throughout the year, since the nature of the habitat and topography in these areas is so different, as described in Chapter 2.

Foods from *Acacia* trees made up a substantial part of the baboons' diet (see Appendix F) and potentially provide an important dry season resource. As one component of baboon food biomass, the availability of these food types is examined with long-term data from this site in the next section.

VARIATION IN ACACIA SPECIES FOOD RESOURCES

At Chololo, four species of *Acacia* tree predominate: *A. etbaica*, *A. mellifera*, *A. tortilis* and *A. nilotica*. Flowers and pods from *A. etbaica*, *A. mellifera* and *A. tortilis* are eaten by the baboons, but only the pods from *A. nilotica*. With data covering a period of 4 1/2 years, from August 1986 to December 1990, it has been possible to examine the reproductive phenology of these *Acacia* species, and to relate variation in their production of baboon food resources to concurrent patterns in rainfall.

Figures 3.9 - 3.12 present data on the production of leaves, flowers and fruits (pods) by each species. Actual counts of the number of flowers and pods present are not available for the whole period for which data were collected. Instead, the data shown here are the mean values of the rating on a scale of 0 - 4 of the presence of these parts (see Chapter 2 and Appendix D for methods of ecological monitoring). Although more crude than an actual count, this measure is straight-forward and provides data across a longer time period. For each species, the relationship between the presence of these parts and rainfall was tested by correlating these data with values of monthly rainfall from the same and previous months. The results of these correlations and the data on the presence of leaves, flowers and pods are first described separately for each species, before the phenology of these *Acacia* species and the implications for baboon food availability are discussed, and the data compared with data from sites in Southern Africa.

Acacia etbaica: Figure 3.9 shows that the presence of *A. etbaica* leaves fluctuated seasonally during 1986 - 1990: for periods of 3 - 4 months, leaf presence was high, followed by periods when the mean value of the rating dropped to levels where leaf coverage was on average only 1-25% (rating = 1). The presence of *A. etbaica* leaves correlated strongly and positively with the amount of rainfall in the previous month ($R = 0.445$, $p < 0.005$) and also, though not so strongly, with the amount of rainfall in the same month ($R = 0.349$, $p < 0.05$). These positive correlations indicate that during and immediately after periods of rain there was likely to be new leaf growth and an increase in the presence of leaves.

Figure 3.9 also shows that *A. etbaica* flowers were present for only short periods (1 - 2 months) and that in most months there were very few or no flowers present. Correlating the presence of flowers with the amount of rainfall in previous months produced a strong positive correlation between the occurrence of flowers and the rainfall 4 months previously ($R = 0.447$, $p < 0.005$), and a similarly significant though weaker correlation with the amount of rainfall 5 months previously ($R =$

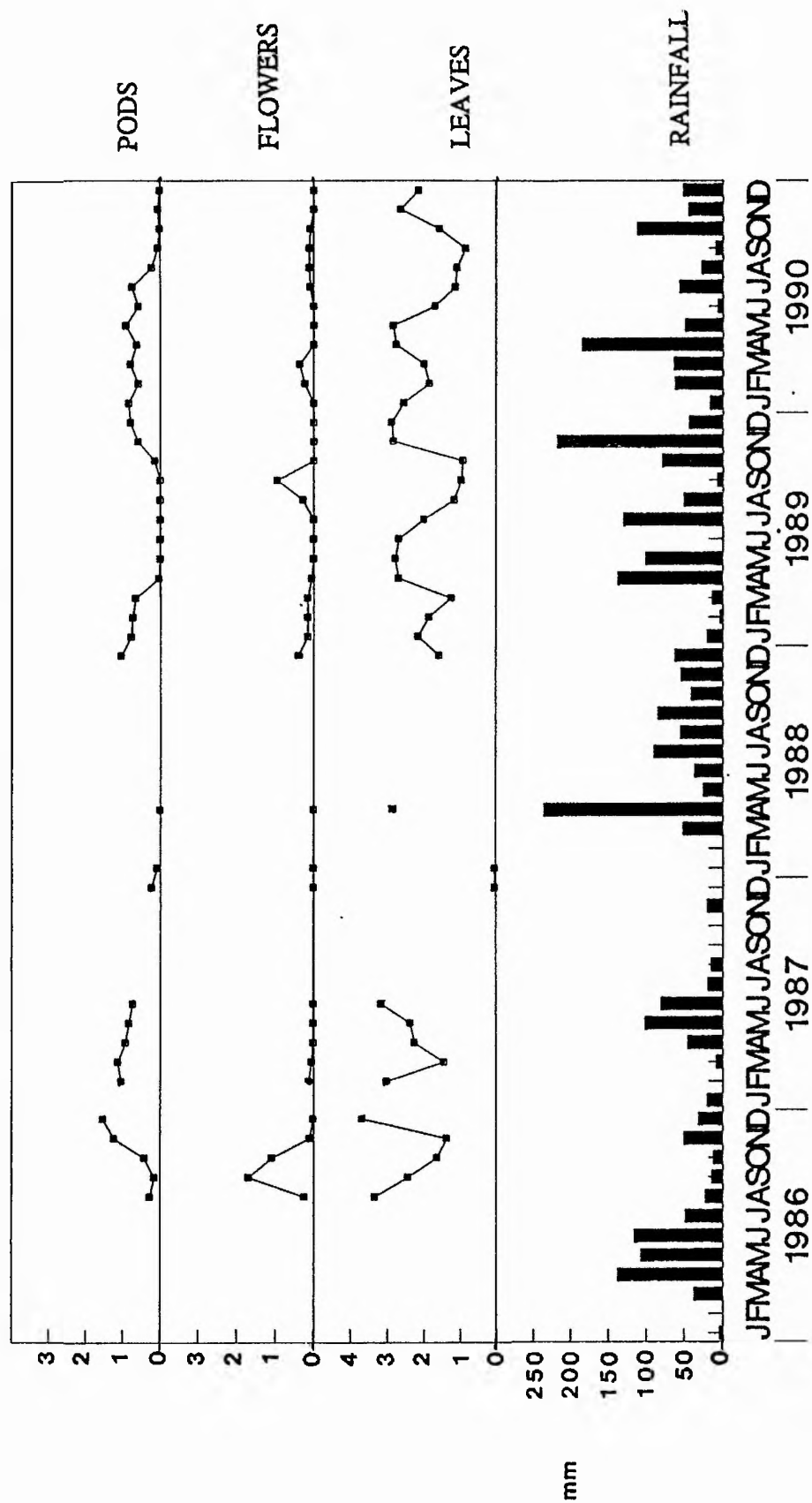


Figure 3.2: Monthly mean values for the presence of *Acacia etbaica* leaves, flowers and pods, and the monthly distribution of rainfall: 1986 - 1990. Presence of leaves, flowers and pods was rated on a scale of 0 - 4 (0%, 1 - 25%, 26 - 50%, 51 - 75%, 76 - 100%).

0.390, $p < 0.01$). Brief seasonal periods of flowering therefore occurred with a lag of 4 - 5 months after periods of heavy rainfall.

A. etbaica pods also exhibited periods of high and low presence, with the onset of their occurrence around November/December. However, there were no significant correlations between the presence of pods and rainfall in the same or previous months. Unlike the flowers, *A. etbaica* pods were present for periods of perhaps 7 - 9 months. The occurrence of pods generally followed a period of flowering (flowers can fail to develop into pods in adverse circumstances), but the long duration of their presence makes it inappropriate to look for a relationship between the presence of pods and patterns of monthly rainfall. (However, using the time of first occurrence of pods in the correlation might reflect the relationship between pod presence and rainfall.)

A. etbaica trees therefore demonstrate a pattern of seasonal variation in the production of leaves, flowers and fruits where the presence of leaves and flowers is closely related to the rainfall experienced, and where a long period of pod presence follows the occurrence of flowering.

***Acacia mellifera*:** Figure 3.10 shows that the seasonal pattern of leaf production exhibited by *A. mellifera* during 1986 - 1990 was similar to that found for *A. etbaica* trees. There was a strong positive correlation between the presence of leaves and rainfall in the same month ($R = 0.405$, $p < 0.01$) and a similar though slightly weaker correlation with rainfall in the previous month ($R = 0.378$, $p < 0.01$). Like *A. etbaica*, leaf production in *A. mellifera* trees occurred immediately after periods of rainfall and the presence of leaves declined during periods of little rain.

A. mellifera flowers occurred for brief periods during 1986 - 1990. Their presence was significantly correlated with the amount of rainfall 5 months previously ($R = 0.280$, $p < 0.05$), which is similar to the timing of *A. etbaica* flower production³. Pods were present seasonally for periods of 6 - 9 months following the occurrence of

³ Although bursts of flower production clearly occur at a time lag following periods of rainfall, the local people in Laikipia use the occurrence of *Acacia* flowers as a predictor of the rains. Figure 3.10 shows that the peaks of flower presence occur in the month before the months of heavy rainfall.

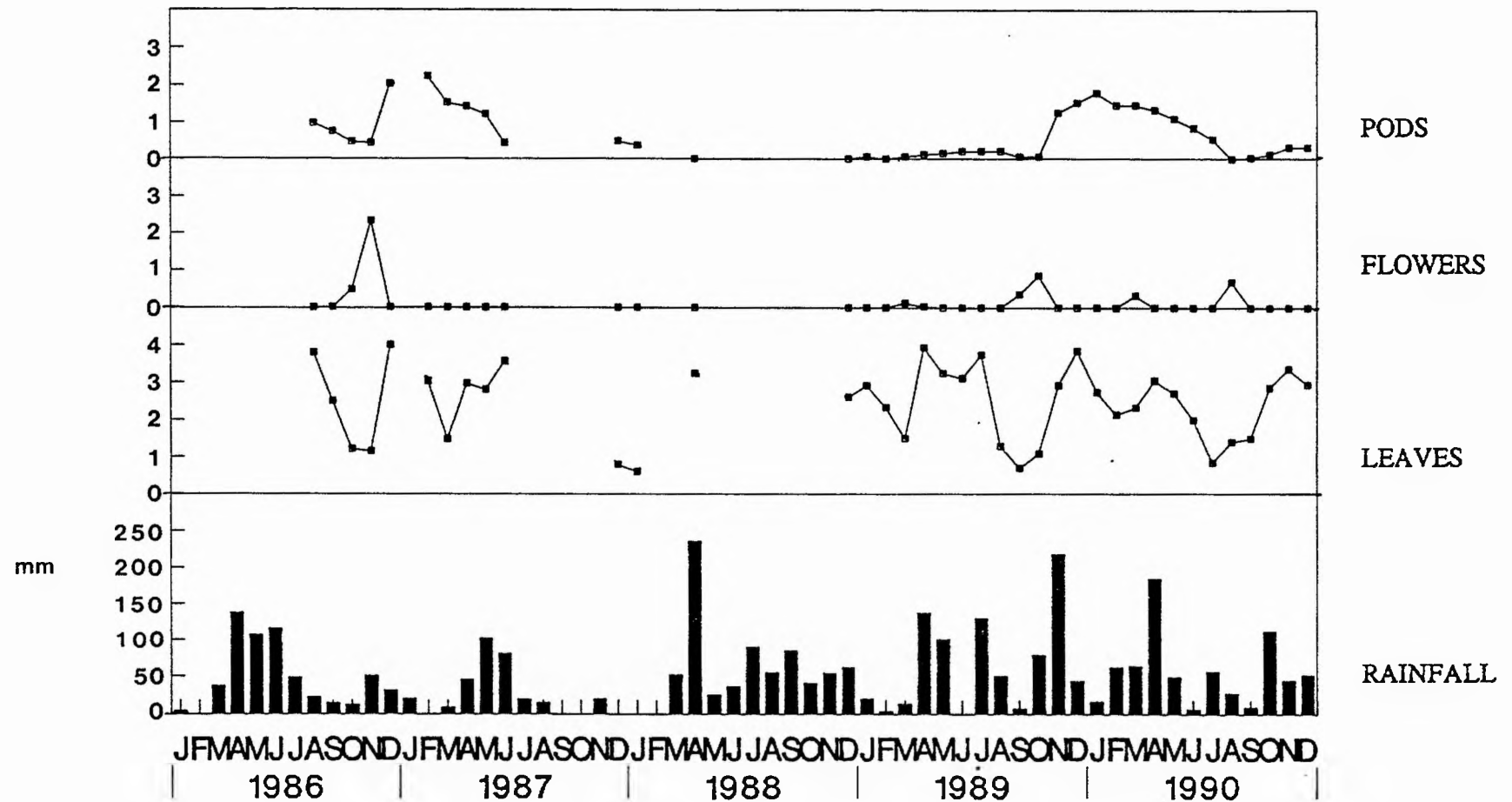


Figure 3.10: Monthly mean values for the presence of *Acacia mellifera* leaves, flowers and pods, and the monthly distribution of rainfall: 1986 - 1990. Presence of leaves, flowers and pods was rated on a scale of 0 - 4 (0%, 1 - 25%, 26 - 50%, 51 - 75%, 76 - 100%).

flowers, though during 1989 the presence of pods was unusually low. Because of the length of the period for which pods were present, correlations between the presence of pods and rainfall were very poor and not significant.⁴

A. mellifera trees exhibit a similar pattern of leaf, flower and pod production to that found in *A. etbaica*. The presence of leaves coincides with periods of rainfall; bursts of flower production occur 5 months after heavy rainfall, and these are followed by the production of pods which remain on the trees for periods of many months.

Acacia tortilis: Figure 3.11 shows that during 1986 - 1990, the presence of leaves and flowers on *A. tortilis* trees followed a similar pattern to that described for *A. etbaica* and *A. mellifera*. The presence of leaves showed seasonal variation, and correlated positively with rainfall in the same month and the previous month ($R = 0.366$ and 0.281 , $p < 0.05$). Flowers were present for short periods, with the peaks occurring at around the same time as those for *A. etbaica* and *A. mellifera*. The occurrence of flowers similarly correlated positively with rainfall 4 and 5 months previously ($R = 0.367$ and 0.285 , $p < 0.05$).

Figure 3.11 shows that the presence of *A. tortilis* pods was low compared with other *Acacia* species, and that they were present for shorter periods of time, 2 - 4 months. Even though the occurrence of pods of this species was more discrete, there were no positive correlations with rainfall in the same or previous months.

A. tortilis trees therefore exhibit a similar reproductive phenology to *A. etbaica* and *A. mellifera* species, where leaves and flowers are produced in response to rainfall, but the availability of pods occurs for shorter periods.

Acacia nilotica: The data presented in Figure 3.12 show that patterns of leaf, flower and pod production in *A. nilotica* are different from those demonstrated for the other *Acacia* species. The presence of leaves during 1986 - 1990 did not show the clear cyclical variation exhibited by the other species. There was no significant correlation between the presence of leaves and rainfall in the same or previous months.

⁴ Correlating rainfall with the presence of only edible pods for all species produced effectively the same results.

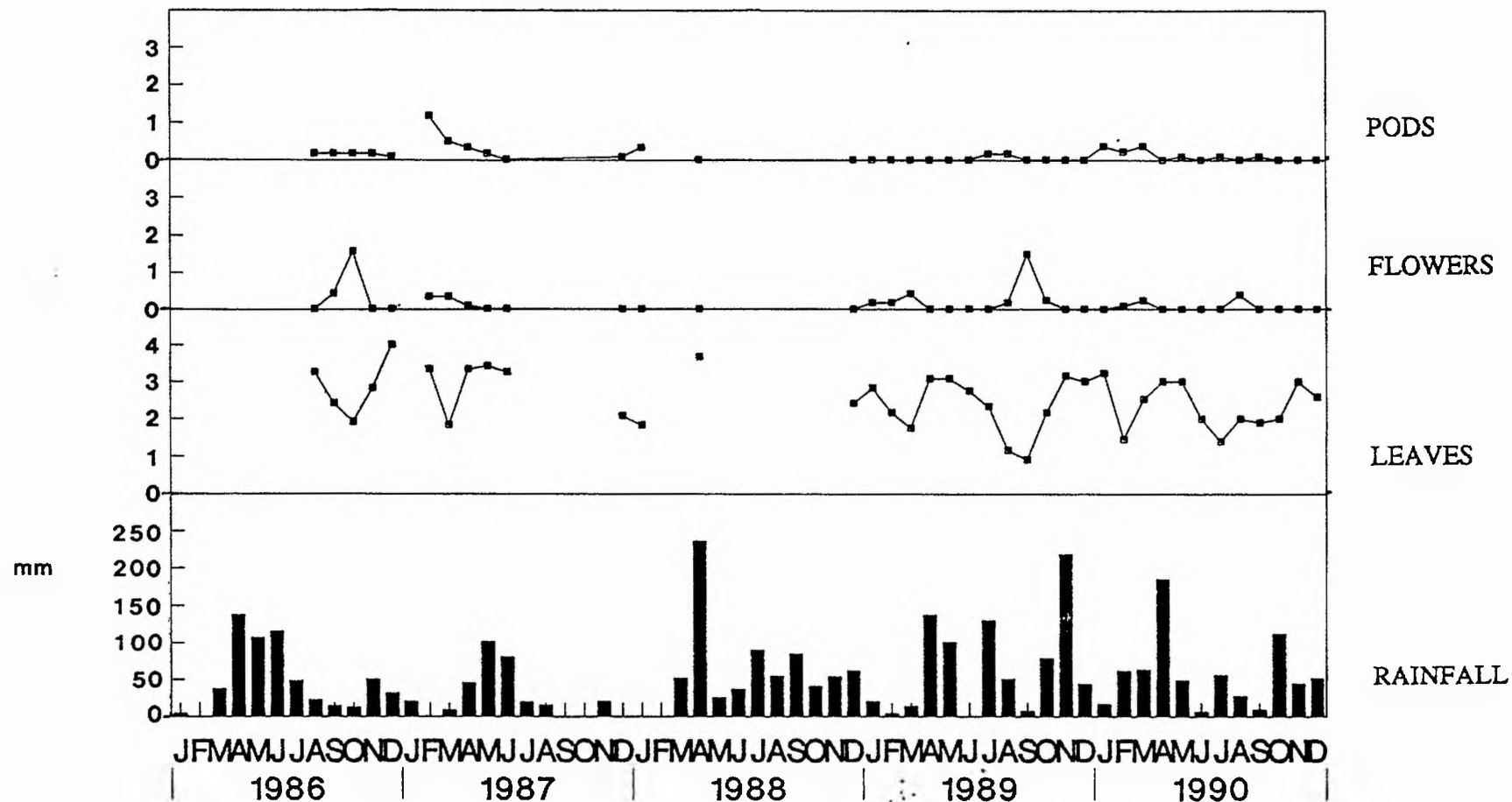


Figure 3.11: Monthly mean values for the presence of *Acacia tortilis* leaves, flowers and pods, and the monthly distribution of rainfall: 1986 - 1990. Presence of leaves, flowers and pods was rated on a scale of 0 - 4 (0%, 1 - 25%, 26 - 50%, 51 - 75%, 76 - 100%).

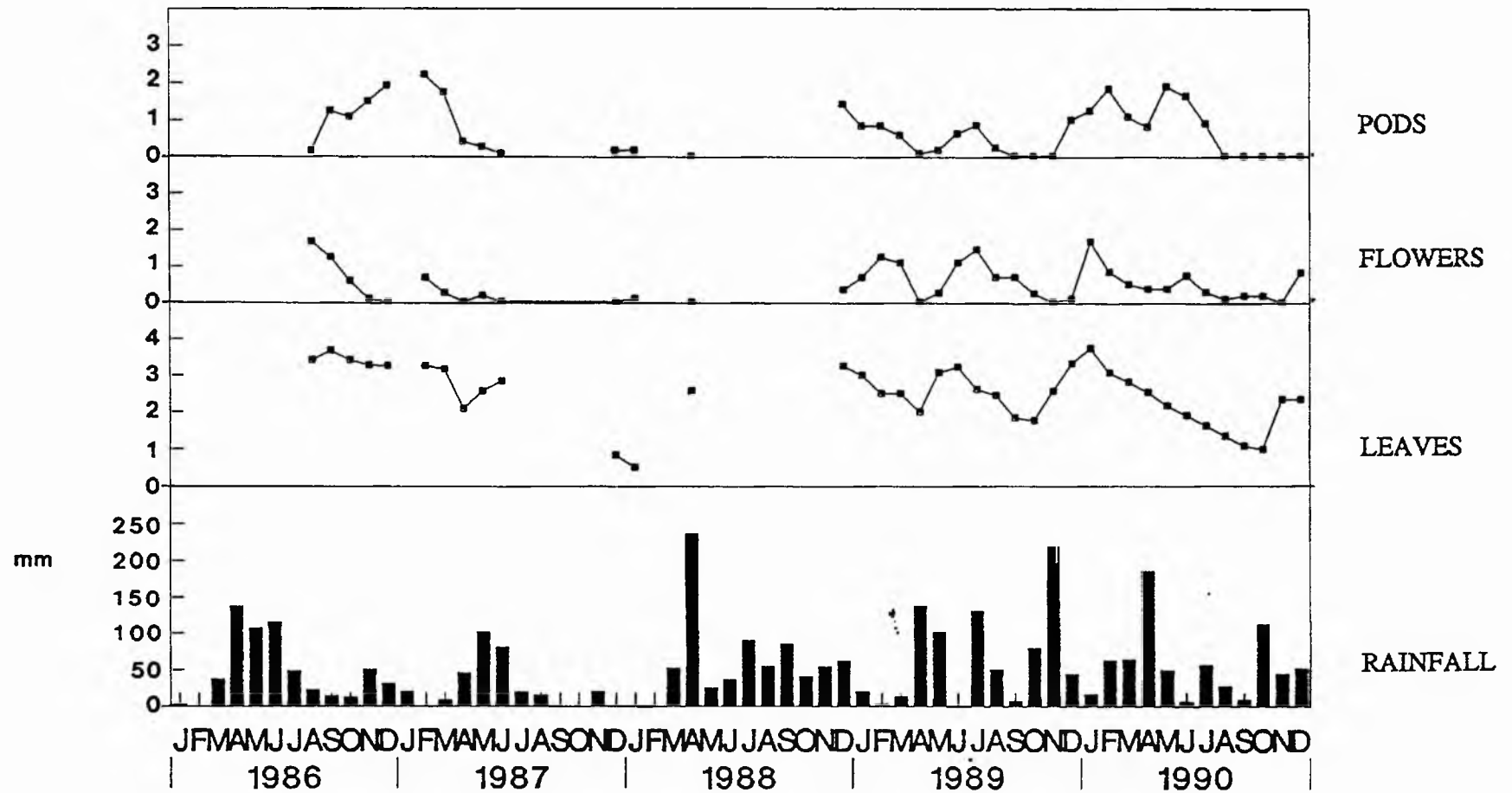


Figure 3.12: Monthly mean values for the presence of *Acacia nilotica* leaves, flowers and pods, and the monthly distribution of rainfall: 1986 - 1990. Presence of leaves, flowers and pods was rated on a scale of 0 - 4 (0%, 1 - 25%, 26 - 50%, 51 - 75%, 76 - 100%).

The presence of flowers was more continuous than in other species, although Figure 3.12 shows that it still varied seasonally. There was a highly significant positive correlation between the presence of flowers and the amount of rain falling 2 months previously ($R = 0.665$, $p < 0.001$), and a similar positive correlation with rainfall 3 months previously ($R = 0.451$, $p < 0.005$). There appears to be a shorter time lag for the production of flowers than in the other *Acacia* species.

The presence of *A. nilotica* pods shows more seasonal variation than the other species described above. Pod presence was high for fairly discrete periods of time following but also coincident with periods of flowering. Unlike the other *Acacia* species, there was a significant correlation between the presence of pods and rainfall distribution, specifically a positive correlation between the presence of pods and rainfall 3 months previous ($R = 0.309$, $p < 0.05$).

A. nilotica trees therefore exhibit strong patterns of seasonal variation where the presence of flowers and pods during discrete periods is closely related to the rainfall in previous months. However, these data on the presence of leaves in *A. nilotica* do not demonstrate a seasonal relationship with rainfall.

The data presented above describe the reproductive phenology of these *Acacia* species. *A. etbaica*, *A. mellifera* and *A. tortilis* have similar patterns for the timing of leaf and flower production in response to rainfall, although pod presence in *A. etbaica* and *A. mellifera* is prolonged compared to the short duration of pod presence in *A. tortilis*. However, the reproductive phenology of *A. nilotica* appears to be different from the other species. The differences between species in the time lag from rainfall to the production of flowers is clear in Figure 3.13 where the values of the correlations between presence of flowers and rainfall in the same and previous 7 months are plotted out for all four species. The shorter time lag for *A. nilotica* results in those flowers occurring during the rainy periods rather than in the dry season as with the other species. *A. etbaica*, *A. mellifera* and *A. tortilis* all have white inflorescences (e.g. Figure 3.14(a)) (although the flowers of *A. mellifera* are larger and longer than the round ones

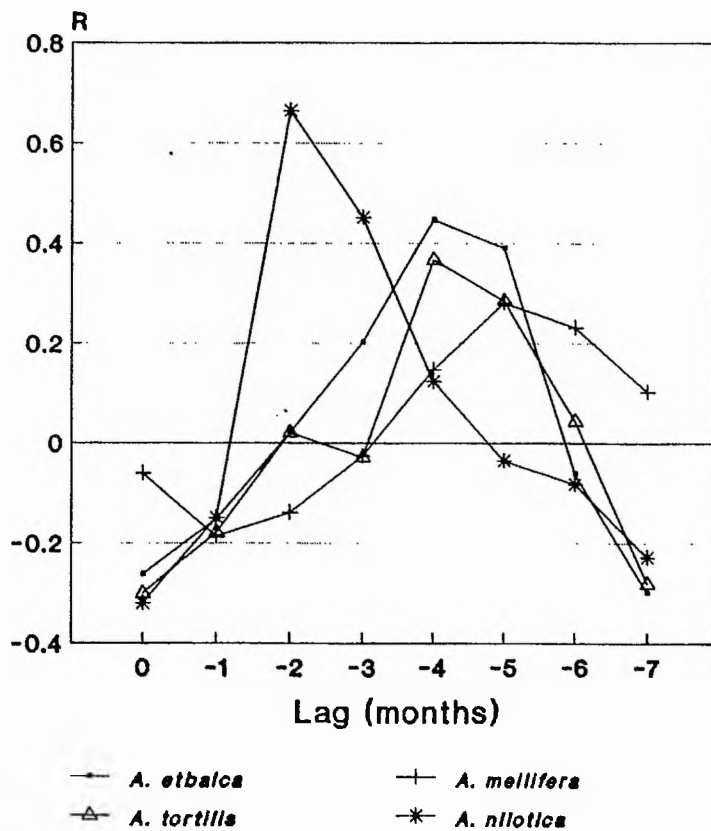


Figure 3.13: Values of Pearson's correlation coefficient (R) from the correlations between flower presence and rainfall in the same and previous seven months for four species of *Acacia* tree.



Figure 3.14(a): The white inflorescences of *Acacia etbaica*: flowering occurs profusely for a short period.



Figure 3.14(b): The yellow inflorescences of *Acacia nilotica*: flowering occurs in flushes a number of times a year on the current season's shoots.

of *A. etbaica* and *A. tortilis*); the flowers of *A. nilotica* are similar to those of *A. etbaica* and *A. tortilis*, but are bright yellow in colour (Figure 3.14(b)). The pattern of pod production is also different in *A. nilotica* from other *Acacia* species. The presence of pods occurred for more discrete periods of time, and followed a seasonal cycle that has been shown to be closely related to rainfall.

Fagg and Barnes (1990) note that different *Acacia* species have different strategies for flowering: *A. tortilis* flowers profusely for a short time to attract large numbers of insects for pollination (see also Figure 3.14(a)); *A. nilotica* flowers in flushes a number of times in the growing season because flowers are produced only on the current season's shoots (Milton, 1987) (Figure 3.14(b)). *A. nilotica* flowering strategy explains the close relationship between rainfall and the presence of *A. nilotica* flowers (though the lack of a similar relationship between the presence of leaves and rainfall in the data for this species is unexpected). It is interesting to note that baboons eat the flowers of *A. etbaica*, *A. mellifera* and *A. tortilis* but do not eat those from *A. nilotica*. Aside from the difference in colour, phytochemical analyses of the flowers of these *Acacia* species (Barton, 1989) may give some indication of why the flowers of *A. nilotica* are not eaten in contrast with those of the other *Acacia* species. *A. nilotica* flowers contain the lowest values of protein (12.8% dry weight) and lipid (3.6% dry weight), and high values of fibre (12.2% dry weight). Probably more influential is the very high level of total phenolics found in *A. nilotica* flowers (10.7% dry weight) which is double that found in other *Acacia* flowers. The more discrete periods of pod presence found for *A. nilotica* could be because the pods from this species (and perhaps *A. tortilis* to some extent) are consumed by animals including baboons as soon as they ripen, and so they are not present for the long periods of time shown by *A. etbaica* and *A. mellifera* pods (hence the good correlations with rainfall), but also, the morphological characteristics of the pods of *A. nilotica* are different from those of the other *Acacia* species, and the methods of dispersal are different (see Fagg and Barnes (1990) and Milton (1987) for details). Unfortunately, it is beyond the scope of this thesis to investigate fully the different reproductive strategies of these *Acacia* species

and the relationship between reproductive parts and predators such as baboons.

The different patterns of flower and fruit production in these *Acacia* species have implications for the availability of baboon foods: the periods when pods and to a lesser extent flowers from different species are present vary slightly throughout the year, staggering the periods of availability and consumption. The occurrence of *A. etbaica*, *A. mellifera* and *A. tortilis* flowers 5 months after heavy rainfall may be a valuable dry season resource for the baboons, at a time when there are few other food resources, as was shown in the previous section with the biomass for 1990. The long-term data on the patterns of flowering described above, show that this flowering regularly occurs in the dry season at Cholulu. However, Figures 3.9 - 3.12 also show that there is variation in the timing and amount of leaf, flower and fruit production between years. For example, in 1989 there were very few *A. mellifera* pods present, and Barton (1989) reports that flowers failed to develop in 1987 (probably because of the low rainfall that year): unfortunately the data for 1987 and early 1988 are too incomplete to properly illustrate this report. The failure of flower production in some years as a result of rainfall patterns, therefore means the non-availability of this potentially vital dry season food resource, and additionally the non-availability of pods later on in the year. Other staple food resources (e.g. in the herb layer) may become available, but if this is not the case, certain periods of food scarcity may become critical.

Examining the data for individual trees, it is clear that trees do not reproduce each year, or that the flowers on an individual tree will necessarily develop into pods. Dunham (1990) found that the seasonal timing of peaks in ripe fruitfall and the mass of the fruit from individual *A. albida* trees fluctuated from year to year. There are clearly opportunities for much further research in this area, on the ecological factors affecting production at an individual level as well as at a broader level.

As mentioned earlier, primate field studies in which data on food availability are collected are still rare. Within the botanical literature, most published work is on the Australian *Acacias* (e.g. Bernhardt, 1989) which are very different from the African

species (Fagg and Barnes, 1990). Much work has been done on pollination and breeding systems of woody legumes (e.g. Arroyo, 1981), and recently this has been extended in preliminary research on the use of managed *Acacia* products as human/livestock resources (Fagg and Barnes, 1990). Detailed botanical studies of growth and reproduction in *Acacia* species have been carried out in Zimbabwe and South Africa (e.g. Milton, 1987; Dunham, 1990, 1991), but the detailed long-term data on patterns of *Acacia* species' leaf, flower and fruit production presented here are unique for sites where long-term baboon research is being carried out. Also, to my knowledge there is no published research on the reproductive phenology of *Acacia* species in an environment which experiences a biannual cycle of rainfall, like that in Kenya, and in which the production of *Acacia* parts is examined with respect to rainfall (though see Fagg and Barnes (1990) for information on the reproductive biology of *A. tortilis* and *A. nilotica*).

Because of the relationships between rainfall and the presence of leaves and reproductive parts, it is particularly interesting to compare the data from Chololo with those from Southern Africa where there is only one rainy period in the year. Data are available for comparison for *A. mellifera*, *A. tortilis*, and *A. nilotica* (Milton, 1987). Figure 3.15 is taken from Milton (1987, Figure 2) and illustrates the patterns of leaf, flower and fruit production for these species that she presents in her study of the phenology of seven *Acacia* species and the effects of browsing on their growth.

The patterns of part presence for *A. mellifera* in South Africa are similar to those observed at Chololo, except that at Chololo, in addition to periods of flowering in September/October (before the rains), there was also the occurrence of flowers in March. At Chololo there were pods present for a longer period of time than in South Africa, and this is probably the result of the double cycle of flowering experienced at Chololo.

Milton's data on *A. tortilis* contrast with those described for Chololo. Figure 3.15 shows that there were flowers present during the rainy season in South Africa, and that there were two consecutive bouts of flowering. Milton's data are consistent with

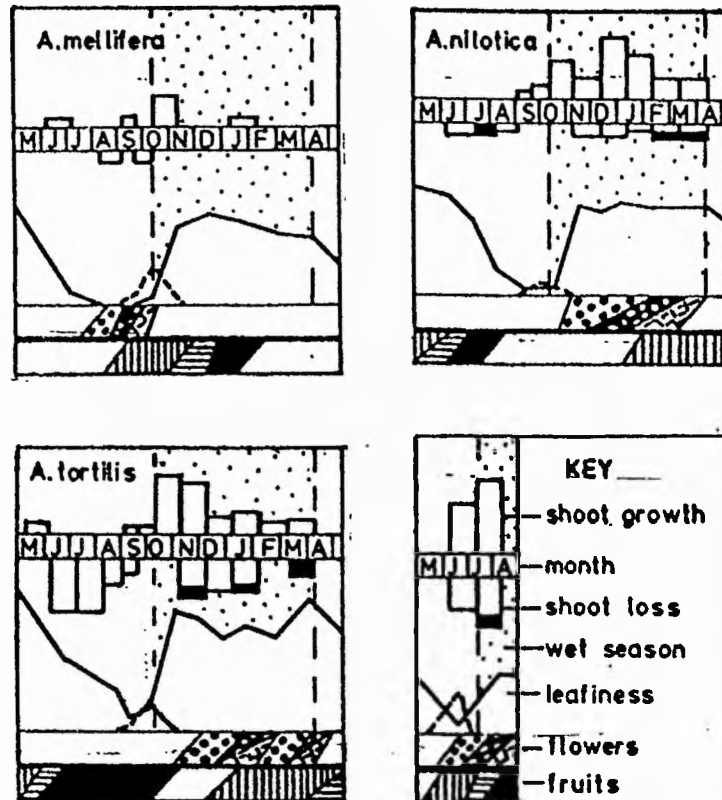


Figure 3.15: Phenology of *Acacia mellifera*, *A. tortilis* and *A. nilotica* at Nylsvley, South Africa, taken from Milton, 1987: Figure 2. Shoot loss = number of marked shoots browsed (white) or dead (black). Flower stages: buds (black dots), open (white dots), withered (hatched). Fruit stages: immature (vertical hatch), mature green (horizontal hatch), ripe pod (black).

the results in Peters, O'Brien and Box (1984) which indicate that *A. tortilis* flowers were found to occur during the rains, and with Post (1982) who reports that baboons at Amboseli ate *A. tortilis* flowers during the short rains (November - January). However, this is not the case at Chololo where *A. tortilis* flowers occurred during the biannual dry season periods. *A. tortilis* pods in South Africa were present for a longer period than at Chololo, perhaps in response to the double flowering period. (The explanation for the brief periods of pod presence at Chololo is not clear, though they may be the result of the pods being rapidly eaten, as mentioned above.)

Milton's data on the phenology of *A. nilotica* show that in South Africa there is a relationship between rainfall and leaf production, whereas at Chololo, no such relationship was found. In South Africa, flowers occurred a couple of months after the onset of rains, which is similar to the time lag found at Chololo, but at Chololo there was a double cycle of flowering. The presence of pods coincident with and following the period of flowering is also similar, though the duration of the presence of pods is longer than the single periods at Chololo.

Many of the differences in the phenology of these species in the different environments can be explained by relating the presence of these parts to rainfall. Leaf presence in South African *Acacias* where there is an annual cycle of rainfall exhibits a single cycle of growth (including *A. nilotica*), compared with the double cycle of leaf presence at Chololo where there is a biannual cycle of rainfall. (Dunham (1991), however, found leaf presence in the species *A. albida* in Zimbabwe was not related to rainfall.) The presence of flowers and pods in *A. mellifera* and *A. nilotica* species also follows a single cycle and the patterns found at Chololo can be seen to be similar but relating to the biannual cycle of rainfall. However, the patterns of presence in *A. tortilis* which at Chololo are very similar to those of *A. mellifera* (and *A. etbaica*), are very different in South Africa. Flower production occurred at a shorter time lag than at Chololo, more like that of *A. nilotica*, so that flowers were present during the rains, and there was even a rapid double cycle of production which occurred in no other species in Milton's study. The latter phenomenon may not be a regular occurrence in

this species, and may just indicate the potential for *A. tortilis* to respond to a period of increased rainfall as is the case with the biannual rainfall cycle experienced at Chololo (though with Milton's data, the period of increased rainfall occurred during the single period of rainfall).

Although data collected once a month represent just a set of 'snap-shots' of the reproductive cycles of these *Acacia* species, it has been possible to demonstrate relationships between rainfall and the phenology of these species, which therefore affect the availability of an important component of baboons' diet. Rainfall is, however, only one factor in a complex of variables which effect *Acacia* tree growth and reproduction. Other factors will be the nature of the soil, local environmental conditions, the occurrence of fires, and the height of the water table (C. Fagg, pers. comm.); temperature (Dunham, 1991); and readily available nitrogen for alkaloids and nonprotein amino acids used in chemical defence (Rundel, 1989). Further research on the interaction of these factors and their effects on the production of food resources will provide valuable insights into understanding such environments. Dunham (1990) reports on the relationship between the amount of unripe fruit of the *A. albida* species eaten by baboons and rainfall, and Wrangham and Waterman (1981) discuss the relationship between vervet monkeys and *A. xanthophloea* products. However, there is still huge potential for research which examines the relationships between plant species, environmental factors and the animals which use their parts as food resources.

CONCLUSIONS

This chapter has shown that there are annual seasonal fluctuations in rainfall and food availability. Monthly values of baboon food biomass do not follow the same pattern of fluctuations as those for other types of biomass, and cyclical periods of resource scarcity and abundance do not necessarily coincide with the dry and wet seasons. However, this methodology specifically provides information on the

availability of food resources which are relevant to the behaviour of baboons. Green biomass cannot be used to predict food availability for baboons.

The measures of biomass were made at the end of each month. In order to have values which are relevant to the behaviour of the baboons during the month, running average values with the previous month have been calculated, and are presented in Figure 3.16. It is these values of baboon food biomass which are used to interpret the impact of seasonality on the behaviour of the baboons in this troop in the chapters that follow.

The potential for analysis of the long-term ecological data from Chololo is huge. Baboon food biomass data from 1986 to the present are available and have not yet been analysed. In particular, with this on-going project, it will be possible to relate long-term fluctuations in baboon foods and the occurrence of vital resources (such as those already shown for *Acacia* flowers and pods) to the demography of this troop of baboons.

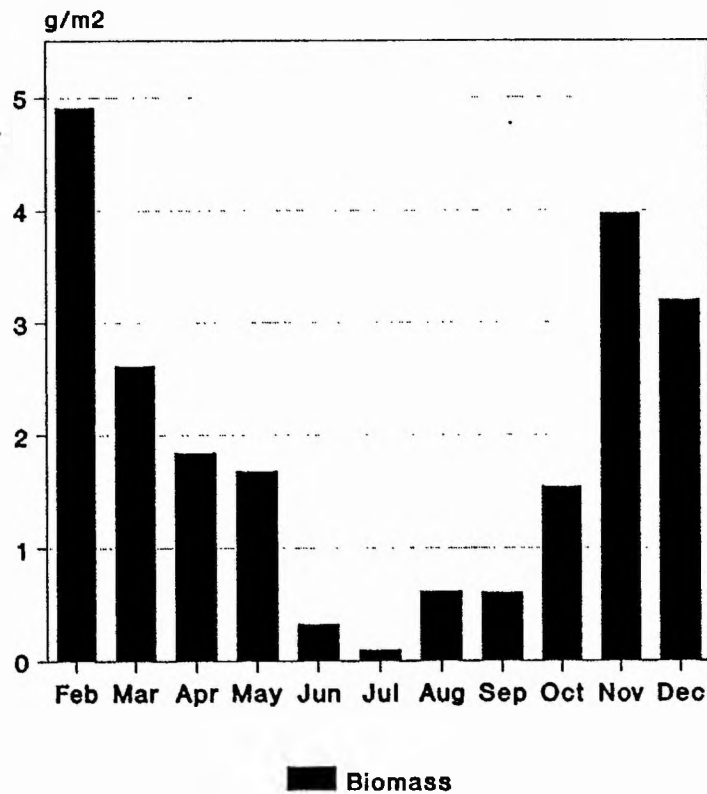


Figure 3.16: Running average values with the previous month for baboon food biomass:1990. These values represent the baboon food biomass available during each month (rather than at the time of ecological monitoring at the end of each month), and are therefore the values that are relevant to baboon behaviour during those months.

CHAPTER 4: RANGING BEHAVIOUR OF THE TROOP

INTRODUCTION

Baboons have been studied in many different environments, varying in the severity of their conditions (see Chapter 1). The size of a troop's home range area and the length of its day journey are related to the quality and distribution of food resources in the environment, and to the number of members in the troop (Dunbar, 1988). Barton (1989) has shown a positive correlation between group size and home range size for *Papio* baboons, whereas the relationship between the size of the ranging area necessary to ensure sufficient food and quality of habitat is negative: ranging area increases as habitat quality decreases (Dunbar, 1988).

The effect of habitat quality on home range area can be seen in data from Amboseli: over a period of 12 years the habitat became more impoverished, and the ranging area of a troop increased from 17km^2 (Altmann and Altmann, 1970) to 40km^2 (Post, 1978) while troop size remained nearly constant. Conversely, a rich habitat such as that provided by a rubbish tip for 'Lodge' troop at Amboseli, requires the troop to maintain only a small home range (less than 4km^2 : Altmann and Muruthi, 1988). Anderson (1982) and Whiten et al. (1987) report large home range sizes for the troops of chacma baboons they studied in the Drakensberg mountains, although since Anderson reports that the vegetation at Suikerbosrand was in fact better than most areas in South Africa, this is likely to involve extreme thermal and altitudinal stress rather than poor habitat quality per se.

Day range length (DRL) is similarly negatively related to habitat quality, and positively to group size (Dunbar, 1988; Barton, 1989). In his analysis to determine the environmental variables which influence behaviour, Dunbar (in press) found that the best regression equation for a set of ranging data from a wide range of different environments included rainfall and group size as factors, and Barton (1989) performed a multiple regression analysis of rainfall and group size on DRL data for *Papio* baboons

in which 62% of the variance in DRL was explained, supporting the idea that baboons have to travel further each day to find sufficient food in poor habitats where availability is low. Aldrich-Blake et al. (1971), for example, report a DRL of 5.8km for the arid environment experienced in Ethiopia which is more than twice that reported by Rowell (1966) for a forest environment (2.4km), and Davidge (1978) reports a DRL of 8.2km for the baboons he studied in an environment of low rainfall that is more than three times that of Rowell's baboons. Difference in group size might be a confounding factor with these data (the troops in Ethiopia and at Cape Point are nearly double the size of the troop studied by Rowell), but looking at similarly sized groups in extremely different environments, the DRL observed by Post (1978) at Amboseli where there was very little rainfall is more than double that observed by Rowell at Ishasha where there was relatively high rainfall. Care should be taken when comparing pairs of data like this because of differences in the techniques used for measuring DRL, and variations in the durations of studies. However, the data from Amboseli, where the effect of group size in conjunction with differing habitat qualities is minimal (and where the same measurement techniques were continuously used), also show that DRL is greater for the later, more impoverished habitat (1963: 5.5km; 1975:6.1km). The difference between these values for 1963 and 1975 is smaller than that demonstrated by the increase in home range size mentioned above: although DRL therefore shows the same effect, it may always be weaker. Whiten et al. (1987) found that although Drakensberg Mountain baboons required a very large home range, a correspondingly large day range was not found, apparently because the group could utilise the large home range by repeatedly moving between a large number of dispersed sleeping cliffs. Altmann and Muruthi (1988) also report that the DRL of their 'Lodge' troop with its enriched environment is much shorter than the comparable value for the other troops at Amboseli.

Although amount of rainfall is a reliable indicator of primary productivity (Coe et al., 1976) and allows the comparison of data between different sites, and monthly distribution of rainfall is closely related to green biomass values (see Chapter 3), it has

been shown that measures of rainfall do not correlate closely with the biomass of available baboon foods (see Chapter 3: Variations in biomass). A measure of total annual rainfall, although denoting the general severity of environmental conditions, therefore does not indicate the additional effects of seasonality on the environment and food availability: at this site there are marked periods of food scarcity, which is typical of savannah environments (in contrast with forest environments). Seasonality and related fluctuations in food resources are potentially crucial factors in an environment, yet very few workers have directly examined these aspects of environmental conditions and the effect they may have on behaviour. If data were available to denote the level of seasonality experienced at the sites used in Barton's regression, we could expect to explain even more of the variance.

Permanent fission, fission-fusion and sub-trooping, although rare behaviour for savannah baboons, can perhaps be viewed as behavioural strategies for coping with severe environmental conditions. Dittus (1988), for example, describes comprehensively four episodes of complete fission in toque macaques within a period of 16 years. Fission was triggered by sudden environmental stress (caused by a cyclone and a drought) and followed the divisions of consistent sub-groups which had existed earlier. Das (1991) describes the potential for fission in rhesus macaque troops in India, and Malik et al. (1985) describe fission in a rhesus monkey group where three new groups were formed.

In 1987, STT troop split into two smaller troops (D. Lochhead, pers. comm.) following a period of drought. This split occurred along lines of 'least genetic resistance' (Nash, 1976; Dunbar, 1988), where related animals stayed together in the newly formed groups. One group was made up of the lower ranking females and their matriline as was observed by Dittus (1988), presumably because these individuals in particular were suffering the increased costs of food scarcity, and the costs were less if they were in a smaller group. Nash (1976) also has reported permanent fission in a troop of baboons at Gombe, though after a long period of instability in the relationships between adult males.

Temporary fission of a large group (herd, band, troop) into smaller parties for foraging during the day has been reported for *Papio papio* (guinea baboon) by Sharman (1981). He notes that even sub-groups often split into smaller foraging units. These smaller groups keep in contact by loud calls (Byrne, 1981). Similar fission-fusion occurs in *P. hamadryas* and *Theropithecus gelada*, where one-male units (based on herding or female coalitions respectively) forage during the day but reunite with the rest of the group at the sleeping cliffs. In these species, membership of the temporary sub-groups ('sub-troops') is consistent. Troop fission which occurs overnight or where groups spend a large amount of time completely separate from each other, and whose membership is largely consistent, can be described as sub-trooping (e.g. Stoltz, 1972). Anderson (1981) denotes 'true' sub-troops as being those where "troops divide frequently and spend all or most of the day completely separate from one another, but the sub-troops are in the process of permanent division into separate troops" (p. 454). One of the troops studied in Botswana by Hamilton et al. (1975) regularly divided into two fragments in this way.

There have been a few reports of sub-trooping in savannah baboons where the troop is dispersed under conditions of poor food availability, and small predator risk (Anderson, 1981). Aldrich-Blake et al. (1971) note that during the day a troop in the arid environment of their site in Ethiopia dispersed into temporary yet non-random groups which moved fairly independently after leaving the sleeping site in the morning. The troop never failed to reassemble and spend the night together and there was considerable coordination in the general pattern of its movement. However, they explained this sub-trooping behaviour as an adaptation to the dry environment where food was scarce and where some dispersal of the troop is then reinforced by the lack of visibility in the scrubland, resulting in spatially distinct groups.

Anderson (1981) reports sub-trooping in the Drakensberg mountains occurring on a seasonal basis, where in the severe cold dry winter months sub-troops were continuously separated, often over more than one day. She interprets this sub-trooping as an adaptation for energy conservation: smaller sized groups need travel a shorter

distance in a day and there is less competition for scarce food resources. She suggests also that particularly vulnerable and more subordinate individuals (e.g. pregnant and lactating females and young juveniles) probably have most to gain by behaving in this way.

In summary, seasonal fluctuations in food availability (temperate or tropical) add to the stress experienced in an environment. Data on seasonal DRLs and behavioural adaptations are scarce, but one behavioural adaptation to a seasonal environment might be sub-trooping. In the sections that follow, data on day range length, home range use and the fission/fusion behaviour of the troop studied are presented and discussed in the context of variation in biomass. The effects of seasonality on the behaviour of the troop of baboons as a whole is examined (the effect of seasonality on individual baboons is discussed in Chapter 7), and these features of behaviour are assessed as adaptive strategies for coping in a seasonal environment.

HOME RANGE AND MEAN DAY RANGE LENGTH OF THE TROOP

The home range size of the troop was estimated from the ranging data of April to October, 1990. All $1/4 \text{ km}^2$ grid squares recorded as having been entered by the troop were summed: squares which were not recorded as having been used but which were completely enclosed were also included. This gave an estimated home range size of 36 km^2 for this 7 month period. This falls within the expected range for *Papio* baboon species (Sharman and Dunbar, 1982; Barton, 1989). Figure 4.1 presents the summed observations of the use of grid squares, with the highest frequencies of observations being at those squares around the sleeping sites (see map of study area in Figure 2.2 for location of sleeping sites).

The estimated home range size is smaller than that observed by Barton during January to December 1986 (43.75 km^2 : Barton, 1989). Since the troop split to form two permanent groups during 1987, a smaller current home range size is consistent with the reduced group size of the troop which I studied. However, estimation of home

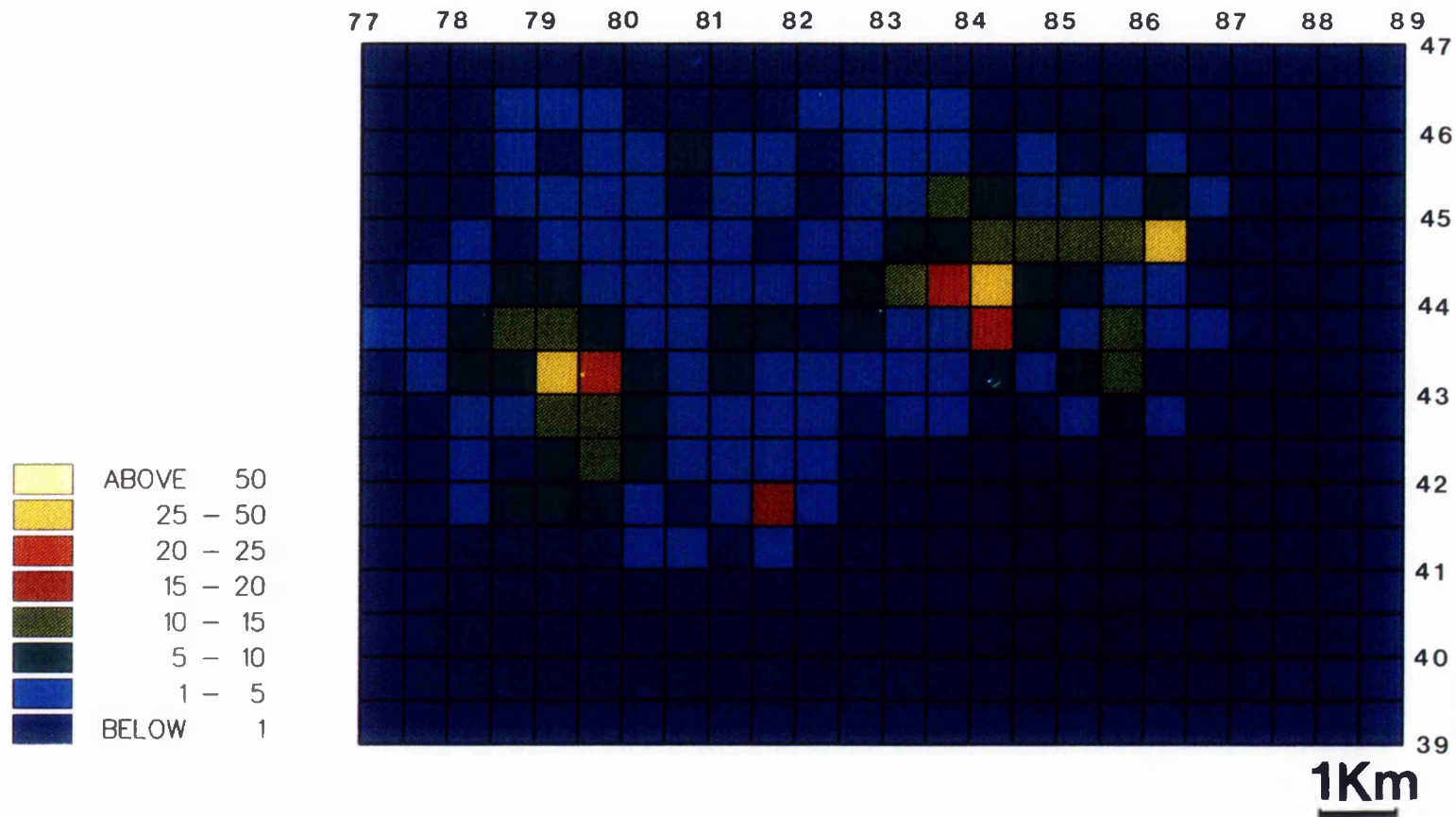


Figure 4.1: Home range area used by STT troop: April - October 1990. The colour scale indicates the frequency with which each 0.25km^2 grid square was observed to be used. The highest frequencies are for squares near the sleeping sites.

range size is based on cumulative data and is therefore related to the duration of time spent observing the troop. Barton (1989) showed that the function is asymptotic, and that 90% of the final value in his study was reached by 7 months (Barton, 1989: Figure 3.7). However, while the cumulative estimate of home range size during the months of observation shown in Figure 4.2 indicate that monthly changes in the estimated home range size generally became smaller, implying an asymptotic curve, it is unlikely that the asymptotic value of home range size for a 12 month period would be reached at a value less than that found by Barton. The sharp increase in size between the months of July and August was due to a shift in home range use and will be discussed in a later section ('Differential ranging on Chololo and the Reserve').

The mean day range length (DRL) across the months April to October was 5.719km (mean of monthly means; SD = 0.965). (N.B. the data for May involved observations on the last two days of the month and so for this analysis were pooled for those for June.) This falls close to the regression line generated by the correlation of DRL and group size for *Papio* baboons (Barton, 1989, from data in Sharman & Dunbar, 1982), indicating that the behaviour of this troop during the study period was consistent with that expected for the genus.

Barton (1989) recorded a mean DRL of 5.637km for STT in 1986. From the relationship between group size and DRL described earlier, one might expect that DRL for the troop in 1990 would be shorter than that found by Barton, because of the decreased troop size (from 103 to 76). Also, in 1990 the total amount of rainfall (690mm) was higher than the mean annual rainfall from 1986 to 1990 (629mm) whereas in 1986 rainfall was lower than the mean value (580mm). Thus, using rainfall as a crude index of habitat quality we might additionally expect mean DRL in 1990 to be shorter than in 1986. DRLs in these two studies were calculated from data collected using different techniques (sampling was every hour in this study compared with every 15 minutes in Barton's). Also, Barton's value for mean DRL was calculated over a period of 12 months, whereas the data in this study are from only part of the year. However, by collecting ranging data less frequently, I would expect the estimates in

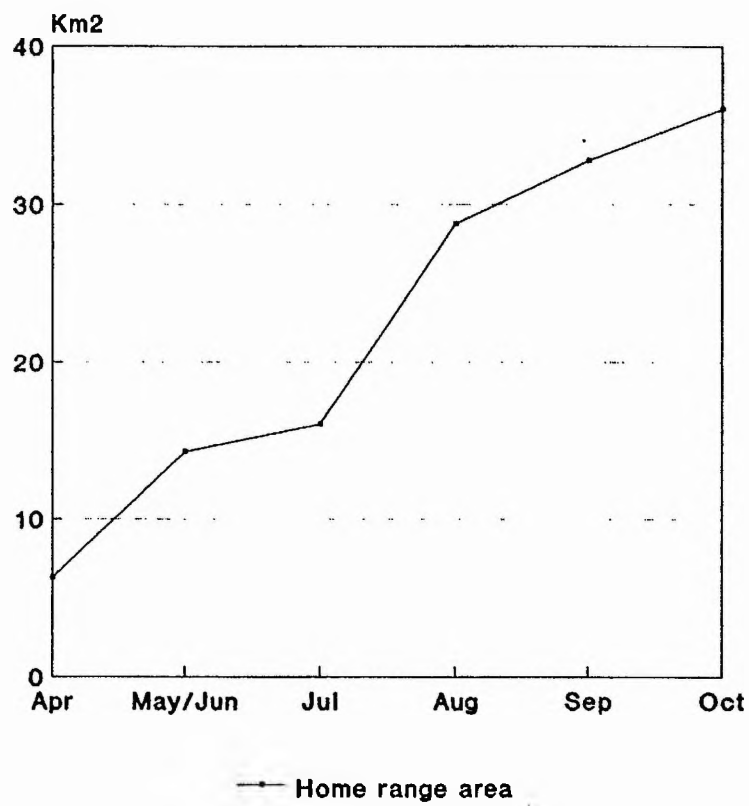


Figure 4.2: Cumulative estimate of home range size (April - October 1990).

this study to be shorter than those based on Barton's technique, so it is likely that there is a greater difference between the mean DRL values than that shown here, and that contrary to expectation, there was a longer DRL for the troop in 1990 even though troop size was smaller.

The mean DRL for days when the troop returned to the same sleeping site across all months is shorter than that for days when the troop travelled to a different sleeping site i.e. intersite DRL (return: 5.300km ($N = 6$, $SD = 0.839$); intersite: 6.053km ($N = 6$, $SD = 1.785$)), though this difference is not significant ($t = -1.22$, $df = 5$, $p = 0.276$). The lack of significance can probably be understood by noting that in some months there are relatively small numbers of observations for days of intersite ranging, and that in the months of May/June and September, the mean return DRLs were actually greater than that of intersite DRLs. Interpretations of this latter point will be discussed in the next section.

VARIATION IN DAY RANGE LENGTH

Table 4.1 presents the monthly mean day range lengths for return DRLs, intersite DRLs, and for the combination of these (all days). The variation in day range length between months (using data from all days) was significantly greater than within months (Kruskal-Wallis test: $H = 11.75$, $p = 0.038$). It therefore becomes of interest to examine monthly variation in DRL with respect to measures of biomass.

Because of the period in each month that ecological monitoring was carried out, the biomass values obtained are estimates of the food available at the end of the month. More relevant to behaviour during a month would be values which represent the biomass in the middle of the month (see Chapter 3: 'Conclusions'): middle of month values were calculated in Chapter 3 by taking running average values with the previous month (Figure 3.16) and used for correlating with behavioural measures. Also because of possible time lag effects, it is advisable to use values of biomass from the end and middle of the previous month and from the end of the month two months previous in such correlations.

Table 4.1: Monthly mean day range lengths for all days, and separately for days when the troop returned to the same sleeping site (Rtn DRL) or travelled to a different sleeping site (Inter DRL): April - October 1990. (Number of days of observation in parentheses.)

Month	All days DRL (N) (m)	Rtn DRL (N) (m)	Intersite DRL (N) (m)
APR	5312 (4)	5237 (2)	5386 (2)
MAY/JUN *	4714 (12)	4902 (9)	4150 (3)
JUL	5217 (11)	5019 (7)	5562 (4)
AUG	5802 (11)	4186 (4)	6725 (7)
SEP	5757 (9)	5826 (8)	5207 (1)
OCT	7513 (6)	6627 (4)	9286 (2)
mean	5719 (SD = 965)	5300 (SD = 839)	6053 (SD = 1785)

* All day mean DRL for May = 4018 (2)
June = 4854 (10)

Monthly $\log(\text{mean DRL})$ values were correlated with estimates of green and baboon food biomass for the middle of the same month, for the end and middle of the previous month, and for the end of two months previous (Table 4.2). (The mean DRLs for May and June were kept separate, although this undoubtedly increased the variance in the data set ($df = 6$): correlation values for data with DRL values for May and June pooled are in parentheses ($df = 5$).)

The correlation values for $\log(\text{mean DRL})$ with green biomass were higher than those with total baboon food biomass. Barton (1989) found a similar phenomenon: although values of baboon food biomass are a more accurate estimation of the amount of food available, measures of green biomass correlate better with patterns of ranging behaviour. This emphasises the importance of food in the herb layer as a staple resource for baboons.

Figure 4.3 is a plot of these correlation coefficients (R) against time lag, and demonstrates that the strongest correlations occurred between DRL and biomass measures in the previous month. For green biomass, the correlation was strongest, and significant at $p < 0.05$, with the middle of the previous month (and also significantly with end of the previous month). For baboon food biomass, the correlation was strongest for the shorter lag - the end of the previous month. The correlation values for the data set with May and June pooled follow a similar pattern, but for both biomass measures the strongest, though not significant, correlations were for biomass in the middle of the previous month.

Few workers have looked at seasonal variation in DRL. Altmann and Altmann (1970) and Post (1978) found no seasonal difference in the length of day journey for troops of yellow baboons they studied in Amboseli, and the data examined by Dunbar (in press) from various different sites indicate that there is no consistent tendency for DRL to be longer in the dry season than in the wet season. However, Altmann (1980) reports that the distance travelled by their baboons was greatest (almost 6km) in September, December and January and lowest (4 - 4.5km) during the long rainy season. At Amboseli, September is clearly the peak of the dry season when food is most scarce,

Table 4.2: Values for Pearson's correlation coefficient (R) for the correlation of monthly mean day range length values with green and baboon food biomass estimates. Values in parentheses are for correlations when data for May and June were pooled together. (N = 7(6))

		R	p
GREEN BIOMASS			
Middle of same month	-0.464	(-0.066)	0.294 (0.901)
End of previous month	-0.816 *	(-0.639)	0.025 (0.172)
Middle of previous month	-0.832 *	(-0.759)	0.020 (0.080)
End of 2 months previous	-0.566	(-0.738)	0.186 (0.093)
BABOON FOOD BIOMASS			
Middle of same month	0.019	(0.510)	0.967 (0.301)
End of previous month	-0.729	(-0.340)	0.063 (0.510)
Middle of previous month	-0.509	(-0.411)	0.243 (0.418)
End of 2 months previous	-0.152	(-0.369)	0.746 (0.472)

* p < 0.05

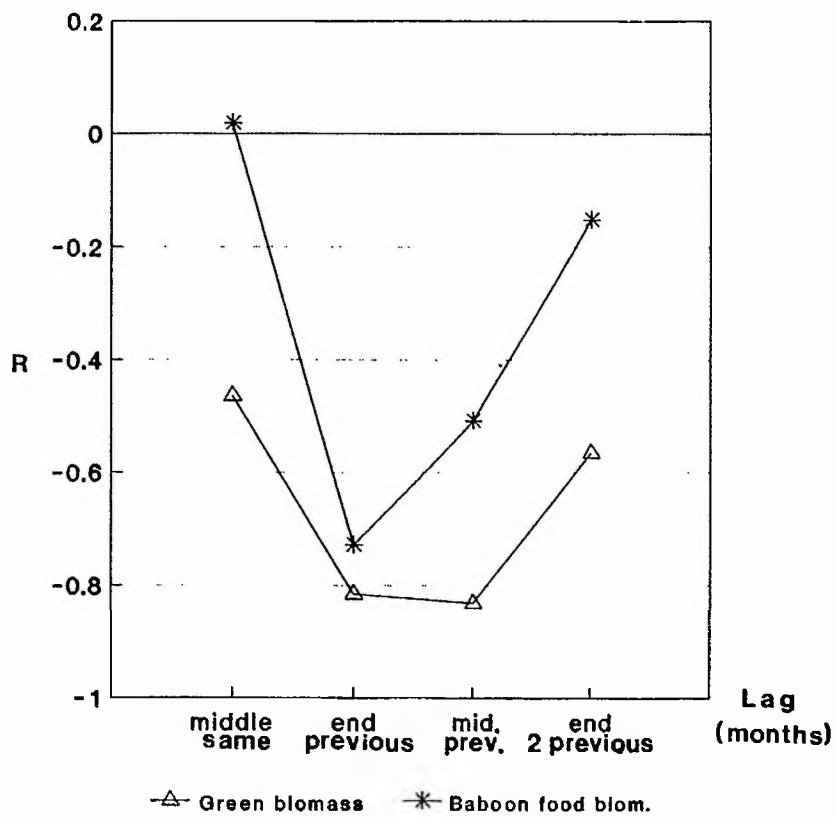


Figure 4.3: Values of Pearson's correlation coefficient (R) from the correlations of green and baboon food biomass with log (mean DRL) for the same month, end and middle of the previous month and end of 2 months previous.

but further explanations would have to be invoked for the long DRL during the short rains of December and January. Anderson (1981), Lee (1983) and Barton (1989) found that the troops they studied travelled further in the dry season when resources were presumably scarce. The negative relationship between DRL and biomass reported here for data collected as the dry season progressed is consistent with this, though the relationship is a delayed one. However, Anderson (1982) also found the adaptive sub-trooping behaviour described earlier which enabled a shorter DRL when conditions were seasonally most harsh.

The shorter time lag in the (marginally significant) relationship between DRL and baboon food biomass is probably related to the different food resources that this measure records (i.e. the inclusion of tree and shrub resources). The period of availability of some of these resources (e.g. *Acacia* tree flowers) may be brief and their influence on DRL therefore more transitory.

Data analysed in Chapter 3 indicate that in August, there was a peak in the availability of *Acacia* flowers. The asynchronous production of flowers by clumps of individual trees during the period of flowering (pers. obs.) probably increased the number of intersite day journeys in August (proportionally more than any other month), as the troop travelled to utilise that particular resource. It would be instructive to correlate DRL with component parts of baboon food biomass (as presented in Chapter 3) to ascertain which resource factors might be influencing length of day journey at different times of year. These analyses are yet to be done.

VARIATION IN RANGING AREA

Mean day range length is an accepted measure of the amount of the home range used by a troop in a day. However, this measure is linear and as such cannot be expected to fully describe the features of daily home range use. For example, it is possible that the length of day journey within a month could remain fairly constant while the particular area used each day varies. Therefore, in such a month, a larger

area of the home range might be utilised than if nearly the same area was used repeatedly each day. As with day range length, it would be expected that such monthly home range area usage would be related to seasonal conditions and food availability.

Ranging data and grid square occupancy were therefore examined by month. An estimate of the size of home range area utilised each month was calculated by noting cumulatively the increase in area being used after each day of observation in a similar way to the calculation of total home range area. These data are presented in Figure 4.4, plotted by number of days since the first observation each month. The curves vary in their gradient and their tendency to be asymptotic.

The number of days of observation of the troop differs each month. In order to make comparisons between the months, the size of home range area at a consistent point in time would have to be considered. This point was chosen to be 30 days after the first observation in the month, thus emulating the behavioural pattern of a month. For each month, the data were plotted and a regression line generated for cumulative area against the log of number of days since first observation. The equations of each regression line were used to calculate a value for the area estimated to be used by the troop during the month by day 30. (Data for May from observation days at the end of the month were pooled with those for June in this analysis as no reliable value for area at 30 days would be calculated from a regression equation generated from 2 data points from the end of the month.) These are presented in Table 4.3. Although some of the estimations generated by this simple method are less than the actual values, differences between the values is not great, which gives confidence in the accuracy of the method.

As with day range length, these values of monthly area use were correlated with biomass measures, namely green biomass and baboon food biomass estimates for the middle of the same month and the end and middle of the previous month. The results of these correlations are presented in Table 4.4.

All the correlations were weak and not significant. The highest correlations were with baboon food biomass estimates for the previous month. However, in contrast with DRL analyses, the strongest correlation for green biomass was values for

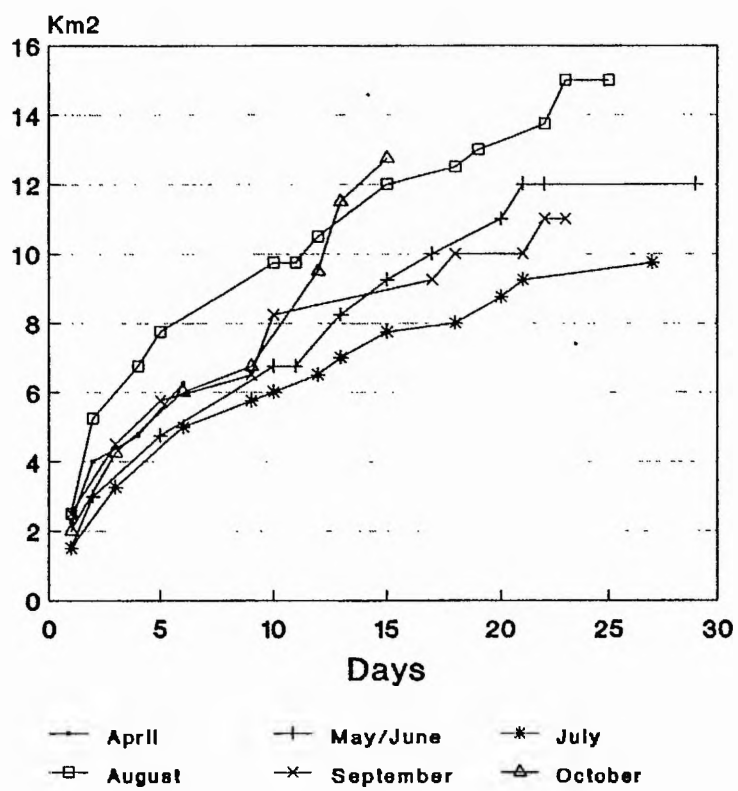


Figure 4.4: Cumulative estimates of monthly home range area.

Table 4.3: Actual and estimated area used by the troop in each month (April - October 1990). For actual areas, N = the number of days in the month that observations covered. Estimations were made for a month of 30 days using the regression equations generated by daily increase in area for each month. (y = area; x = day number since first observation)

Month	Actual (N) area (km ²)	Estimated area (km ²)	Regression equation
APR	6.25 (6)	9.35	y = 2.310 + 4.765 log x
MAY/JUN	12.00 (29)	11.80	y = 0.376 + 7.735 log x
JUL	9.75 (27)	9.37	y = 0.709 + 5.866 log x
AUG	15.00 (25)	14.68	y = 2.679 + 6.845 log x
SEP	11.00 (23)	11.13	y = 1.748 + 6.354 log x
OCT	12.75 (15)	13.27	y = 0.819 + 8.428 log x

Table 4.4: Values for Pearson's correlation coefficient (R) for the correlation of monthly estimated area values with green and baboon food biomass estimates. (N = 6)

	R	p
GREEN BIOMASS		
Middle of same month	-0.395	0.438
End of previous month	-0.337	0.514
Middle of previous month	-0.332	0.520
BABOON FOOD BIOMASS		
Middle of same month	-0.013	0.980
End of previous month	-0.457	0.361
Middle of previous month	-0.514	0.297

a shorter time lag, the middle of the same month. The sign of these weak correlations is consistent with the negative relationship between monthly variation in biomass and DRL described above, implying that when resources are scarce, the baboons are required to use a larger area to gain sufficient food. These data suggest that although the amount of green biomass has a time lagged effect on DRL, it has a more immediate effect on the area being used in a month.

However, these weak correlations indicate that the relationship between ranging behaviour and biomass is complex. The areas estimated as being used by the troop each month (Table 4.3) demonstrate that there is not just a simple relationship with quantity of resources: for example, the area being utilised in August is much larger than that for July.

Frugivores require a larger ranging area than folivores because of the patchy nature of their primary food resource (Dunbar, 1988). It is more than feasible therefore that the nature of the main food resource being exploited by an omnivorous animal in any month would affect the amount of the home range being utilised in that month. I have already noted the importance of *Acacia* flowers in the diet of the troop in the month of August, and would predict that as with DRL, the nature and patchy temporal and spatial distribution of this dry season food resource had a strong effect on the greater size of area that the troop needed to exploit that month. Data from at least 12 months and several dry season cycles is really necessary to confirm these predictions, in conjunction with data on fluctuations in actual baboon food biomass such as those recorded at this site. Also, correlations of these estimated areas with components of the baboon food biomass values would be interesting, to see the effect of individual resource types on area use.

With more data it would also be interesting to examine the rate at which the area utilised in a month is accumulated. It is predicted that when resources are patchily distributed (flowers, fruit), the cumulative area used in a period, for example a month, would increase rapidly, because once an area's resources are exhausted (for example, a grove of trees, whose food content a troop could consume in a few hours), the troop

has to move on to the next area. A resource of more homogeneous distribution would not be so quickly exhausted in an area, and then a shorter distance would be necessary to travel to the next area.

There are differences in the size of the home range area utilised in each month for April to October 1990. The areas within the home range that were used also varied, as illustrated by the monthly break down of the total home range data in Figure 4.5. This is discussed further in the next section.

DIFFERENTIAL RANGING ON CHOLOLO AND THE RESERVE

During 1990, STT troop ranged in areas on both the Reserve and Chololo. The number of nights spent each month at each sleeping site within their home range area are detailed in Table 4.5. These data are presented graphically in Figure 4.6 with the location of the sleeping sites categorised as being on Chololo or on the Reserve (for distinction between Chololo and the Reserve, see overlay on Figure 2.2).

From these data it is clear that the troop did not use the home range uniformly throughout the year. In August there was a shift in ranging which involved the troop sleeping almost entirely at sites on Chololo, after mainly sleeping on the Reserve for the first 7 months of the year. This pattern of behaviour can also be seen in the cumulative estimate of home range size (Figure 4.2) where between the months of July and August, there is a sharp increase in the home range area being used

From the ranging data of April to October, I calculated the number of times the troop was recorded as having entered each of the $1/4 \text{ km}^2$ grid squares in the home range that had been used during the month. Each square was assigned as being on Chololo or on the Reserve (as defined in Chapter 2 Figure 2.2), so the percentage of time spent in each area could then be calculated. These data are presented in Figure 4.7, and again show clearly that during August and the subsequent months, the troop spent more time on Chololo than on the Reserve, in contrast with their behaviour in earlier months.

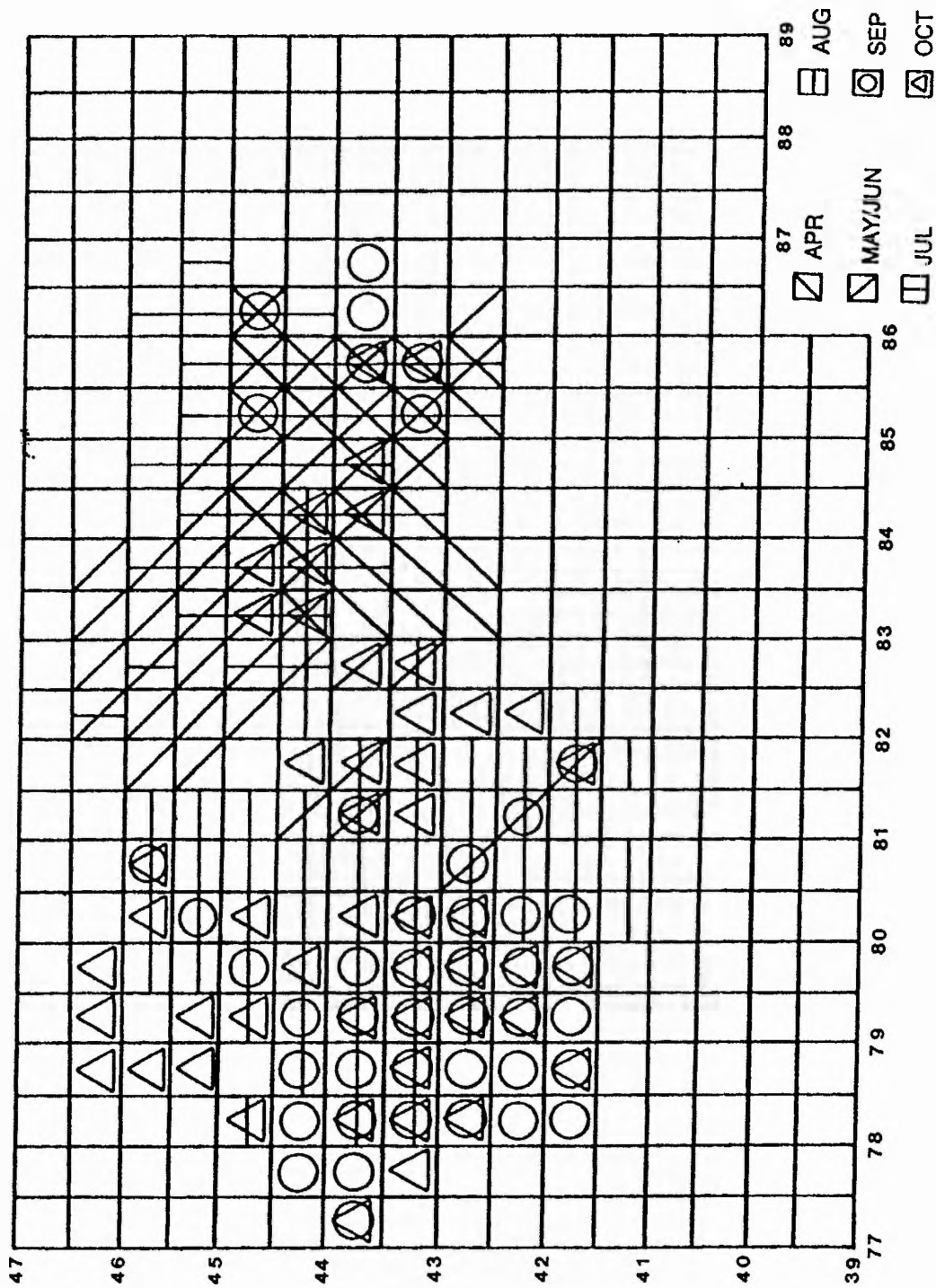


Figure 4.5: Area of the home range used in each month: April - October 1990.

Table 4.5: The number of nights spent by the whole troop at each sleeping site (January - October 1990).

Month	N	RESERVE			CHOLOLO				?
		FTG	WR	MUS	RR	MALI	OR	OLD	
Jan	19	19							
Feb	23	11	8		2				2
Mar	13	13							
Apr	18	5	13						
May	16	2	11						3
Jun	24		19	1	2				2
Jul	28	18	8	1					1
Aug	24		1		6	12	2	1	2
Sep	19					18	1		
Oct	12		2		1	9			

Key: FTG = Fever Tree Gully; WR = White Rocks; MUS = Musul;
RR = Rough Rocks; MALI = Mali; OR = Ostrich Rocks;
OLD = Ol Doyne; ? = sleeping site unknown

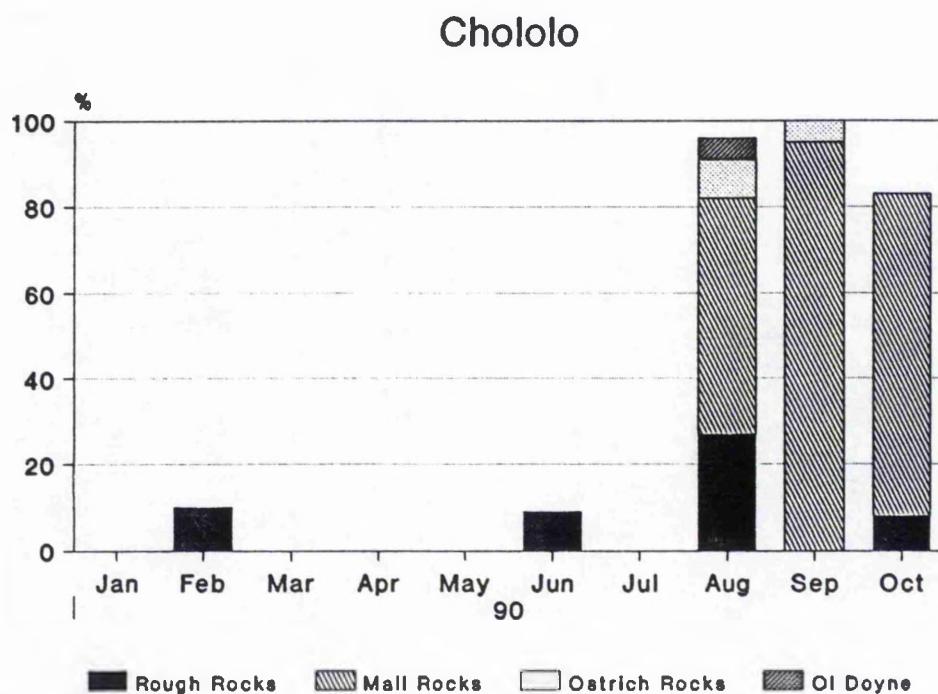
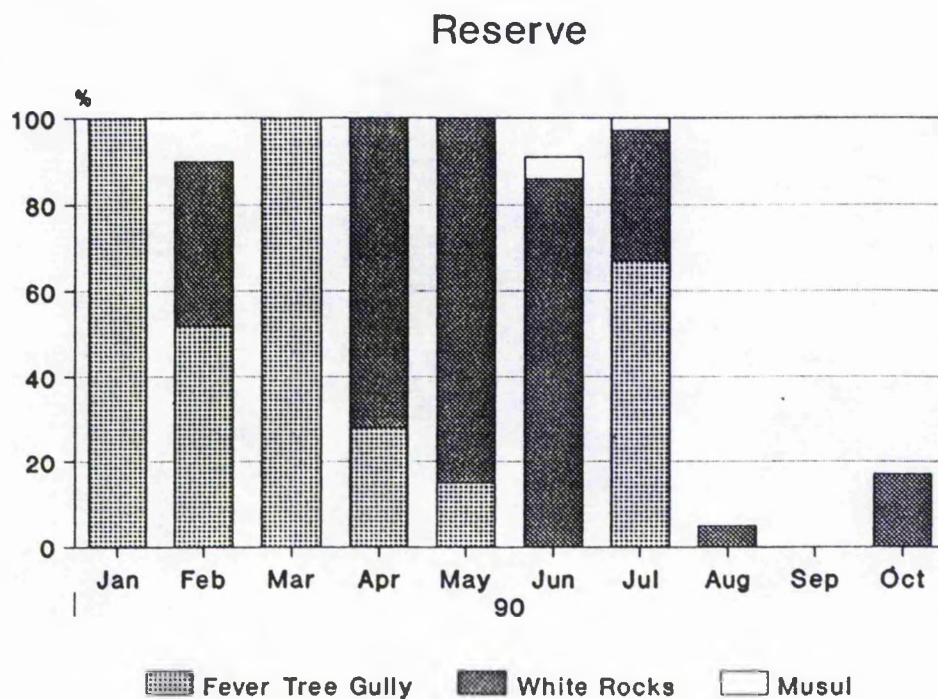


Figure 4.6: Monthly distribution of use of sleeping sites on the Reserve and Chololo based on nights where the troop was observed sleeping together at one site (omitting nights when location of the site was unknown).

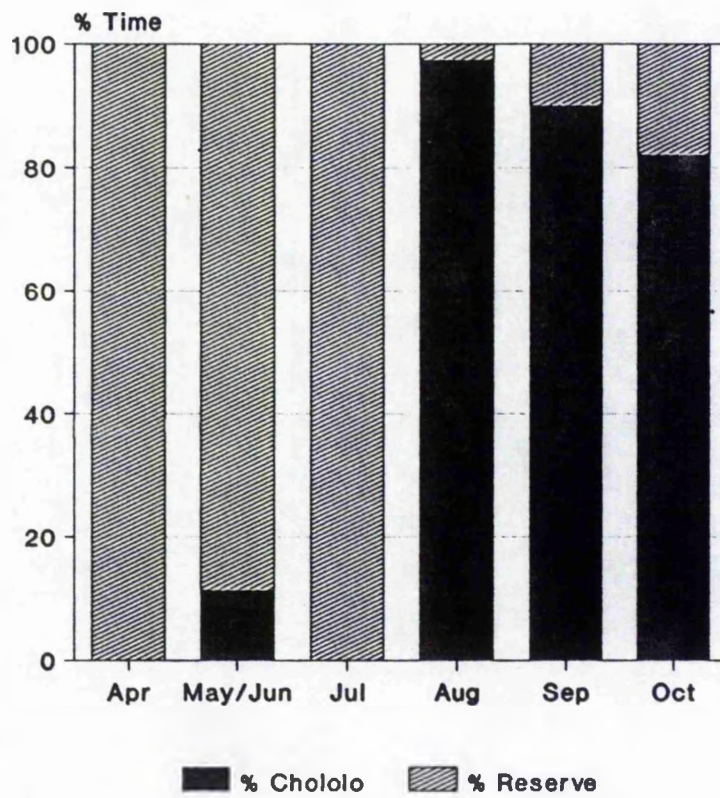


Figure 4.7: % Time spent ranging on Chololo and the Reserve: April - October 1990.

This behaviour has to be viewed in the context of the seasonality of this environment and the food resources which were available. Although spatial analyses of the biomass of baboon foods available have not yet been carried out (see Chapter 3), Figure 3.3 shows that in August, *Acacia* flowers were an important component of the biomass available. Appendix F indicates that *Acacia* flowers were in the top 10 foods eaten in August/September.) Examining the monthly distribution of *Acacia* flower biomass for Chololo and the Reserve separately, there is a large difference between the biomass of *Acacia* flowers available in August in these two areas: the biomass of flowers is very much greater on Chololo than on the Reserve (Figure 4.8). It seems likely that the troop shifted their current ranging area when these flowers became abundantly available on Chololo in comparison with their availability on the Reserve.

Whiten et al. (1987) note that baboons in the Drakensberg Mountains retreated seasonally from some areas in their home range (due to severe temperatures). Henzi et al (in press) report that these troops also used some areas of their home range preferentially, influenced by the spatial distribution of food. They conclude that this behaviour reflects the severity and seasonality of the environment at that site.

At Chololo, varied use of the home range area can also be viewed as a coping strategy for living in a seasonal environment. Chololo and the Reserve differ in the nature of their vegetation (see Chapter 2), with the Reserve having more arid adapted plants due to its position in relation to the rainfall gradient of the area (Strum, pers. comm.). However, in the dry season, fewer resources tend to be exploited (Post, 1982; Barton, 1989), and it has been suggested (in Chapter 3) that *Acacia* flowers are one such food which is important as a resource in the dry season. Ranging behaviour which allows such resources to be incorporated into the baboons' diet would therefore be adaptive. Full analysis of the biomass data and the spatial and temporal availability of especially dry season food resources would determine the effect such resources have on ranging behaviour, and whether, as seems to be the case, a strategy of seasonal shifts in response to food availability is occurring in this marginal area.

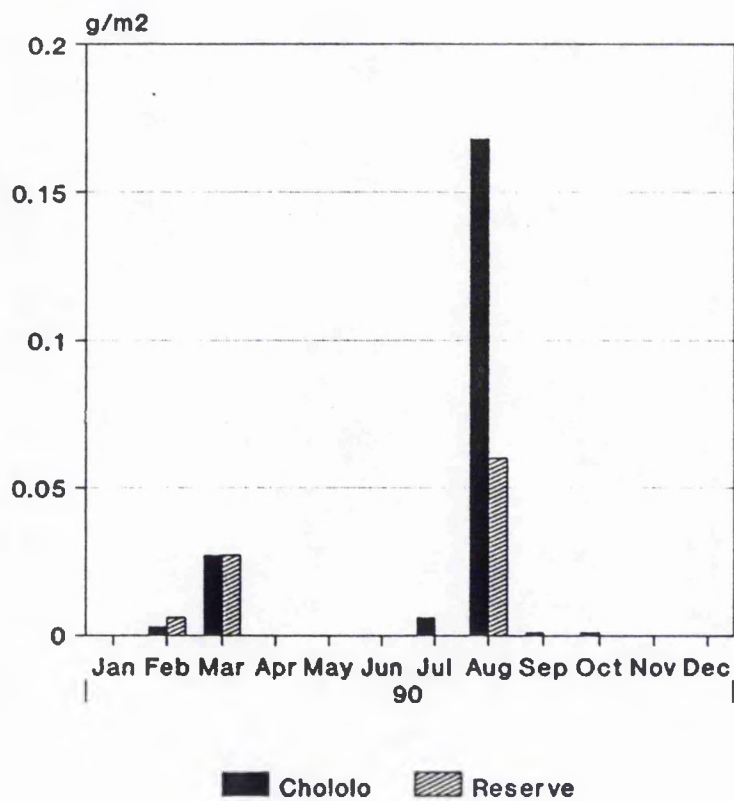


Figure 4.8: Monthly distribution of *Acacia* flower biomass: 1990.

TEMPORARY SPATIAL SEPARATION IN THE RANGING BEHAVIOUR OF SUB-GROUPS WITHIN THE TROOP

During 1990, I observed STT split into two and sometimes three sub-groups. The smaller groups were known as STILTON's group and OTIS's group after the males who appeared to lead them. The apparent leader of 'the rest of the troop' group was EUPHORBIA, the highest ranking female. These groups often ranged separately and on some occasions slept at separate sleeping sites. Table 4.6 lists the nights when members of the troop slept separately at different sites. Within the home range of the troop, there was no shortage of sleeping sites, so that did not act as a constraint to force the baboons to unite, as has been found at some sites where sleeping sites are a limited resource (hamadryas baboons: Kummer, 1968).

The composition of the sub-groups remained fairly constant. Figure 4.9 describes the membership of STILTON's group, based on three censuses carried out when it was realised that the troop had divided. The last census, made when the troop had been separated for several days, is thought to represent the core members of this group. All members present in that census had been present in at least one other census and most had been present in all three of them. STILTON was consistently the only adult male in the group. Even within the main group of STT he was usually to be found with a predictable group of adult females and their offspring around or near him. These adult females included 8 out of the possible 20 adult female members of the troop. Seven out of the 8 subadult females in the troop were with him in 2 out of 3 of the censuses carried out.

Following Anderson's definition involving independent ranging behaviour, and with the consistent membership that the groups show, these sub-groups within STT can be seen to be sub-troops (though it is yet to be seen whether the sub-troops are in the process of permanent division, which would then comply fully with Anderson's definition of 'true' sub-troops).

Although the troop generally slept together as one group (with the exception of the dates noted), the ranging behaviour of these sub-troops was not coordinated. Often

Table 4.6: Details of the nights where STT slept simultaneously at more than one sleeping site

<u>Night of</u>	<u>SI's group</u>	<u>Rest of troop</u>	<u>OT's group</u>
12 April	WR	FTG	
? 7 May	??	FTG?	
?19 May	??	WR	
?26 May	ER?	WR	
?30 May	??	FTG	
12 June	WR	FTG	
23 July	FTG	WR	
8 September	Mali	RR	
10 September	WR	Mali	
11 September	FTG?	Mali	
12 September	FTG	Mali	
13 September	FTG	Lab	
14 September	FTG?	OR	
15 September	FTG?	Mali	
5 October		RR	Mali
8 October	RR	Mali	
11 October		??	Mali
12 October		FTG	??
13 October	FTG	WR	RR
22 October	(abnormal groups - RR & ??)		
23 October	OR	??	??*
24 October	RR	Mali	

Sleeping sites: WR = White Rocks; ER = Euphorbia Rocks; FTG = Fever Tree Gully; Mali = Mali; RR = Rough Rocks; OR = Ostrich Rocks; Lab = Labasoit; ?? = unknown

* OT, TW, TT, TX only

12 APRIL 1990

Adult males	ST							
Sub-adult males	DJ	RZ						
Adult females	DN	LZ	MD	MI	MR	NI	OP	TR
Sub-adult females	AL	AM	CN	GT	JN	KY		
Juvenile males	GG	IN	JY	MI	MJ	NK	NR	SA
Juvenile females	BE	DK						
Infant males	NP	PO						
Infant females	DH	LN	MC	MO	MT	TY		

N = 35

23 JULY 1990

Adult males	ST							
Sub-adult males	DJ	IL	RZ	YN				
Adult females	AL	KH	LZ	MD	MI	MR	OP	TR
Sub-adult females	AM	CN	DK	JN	KY	VS		
Juvenile males	JY	MI	NK	NR	TO			
Juvenile females	BE							
Infant males	PO							
Infant females	AH	LN	MC	MO	MT	TY		

N = 32

10 - 15 SEPTEMBER 1990

Adult males	SI							
Sub-adult males	DJ							
Adult females	AL	LZ	MD	MI	MR	NI	OP	TR
Sub-adult females	AM	CN	GT	KY	VS			
Juvenile males	JY	MI	NK	NR				
Juvenile females	BE							
Infant males	PO							
Infant females	AH	LN	MC	MO	MT	TY		

N = 27

KEY: bold type = present in two out of three censuses
 ○ = present in all three censuses
 □ = born during 1990
 / = died during 1990

Figure 4.9: Composition of Stilton's group on three occasions when they split from the rest of the troop: individuals are listed alphabetically in age-sex categories.

during a day of following the troop, I became aware that part of the troop was 'missing'. In thick *Acacia* woodland, it was perhaps impossible to locate the sub-troops until they had reunited at a sleeping site. On some days when I was in the field with King'waa or a member of U.N.B.P. staff, we could record the troop as being dispersed over as much as 2km. On days when the sub-troops slept at different sleeping sites, for example in September, they may have been ranging as much as 8km apart. If members of the same matriline were separated while the sub-troops were ranging apart, there would often be barks and calls, but when the sub-troops were reunited after sleeping apart, very few strong reactions between members were perceived, other than perhaps a period of grooming, depending on the time of day of the reunion. Figure 4.10(a) indicates the ranging behaviour of the sub-troops in September 1990. The pattern for October 1990 (Figure 4.10(b)) is more confused, with three subgroups present at times, and data on individuals present harder to obtain.

The sub-trooping behaviour of STT is still in progress (King'waa, pers comm.), and so is unresolved. It is possible that these sub-groups are sub-troops in the process of "permanent division into separate troops" (Anderson, 1981): if conditions become more extreme, for example in another drought as experienced in 1987, then the increased environmental stress would trigger another split of STT into smaller troops along the lines of the consistent subdivisions already present. Dunbar (in press) suggests that groups whose time budgets are under stress because of environmental conditions (including seasonality) are able to spend less time than they need to socially interacting, and are therefore less socially cohesive, and more likely to fragment into smaller parties for foraging or permanently split. The increased occurrence of sub-groups sleeping separately as the dry season progressed (the rains came after October 17th), and as this area experienced periods of food scarcity (see data presented in Chapter 3), suggests that this behaviour is in fact seasonal sub-trooping, and an adaptation in a strongly seasonal environment to such periods of resource scarcity. At such times the advantages of being in a small troop (short DRLs and energy conservation, while acquiring sufficient food) become pertinent. By contrast, in August

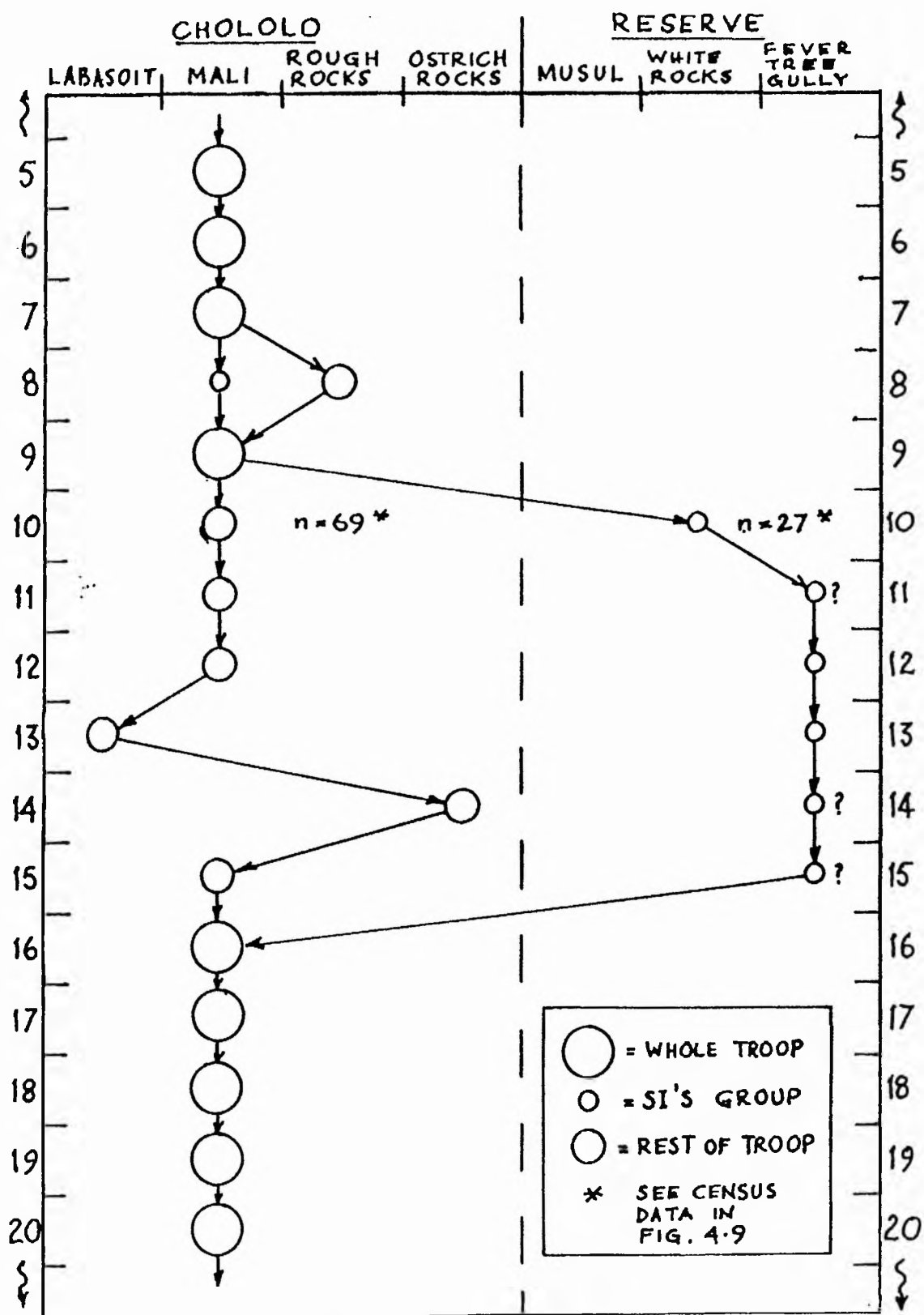


Figure 4.10(a): Fission/fusion of STT troop: sites at which the troop slept together and as separate sub-troops during September 1990.

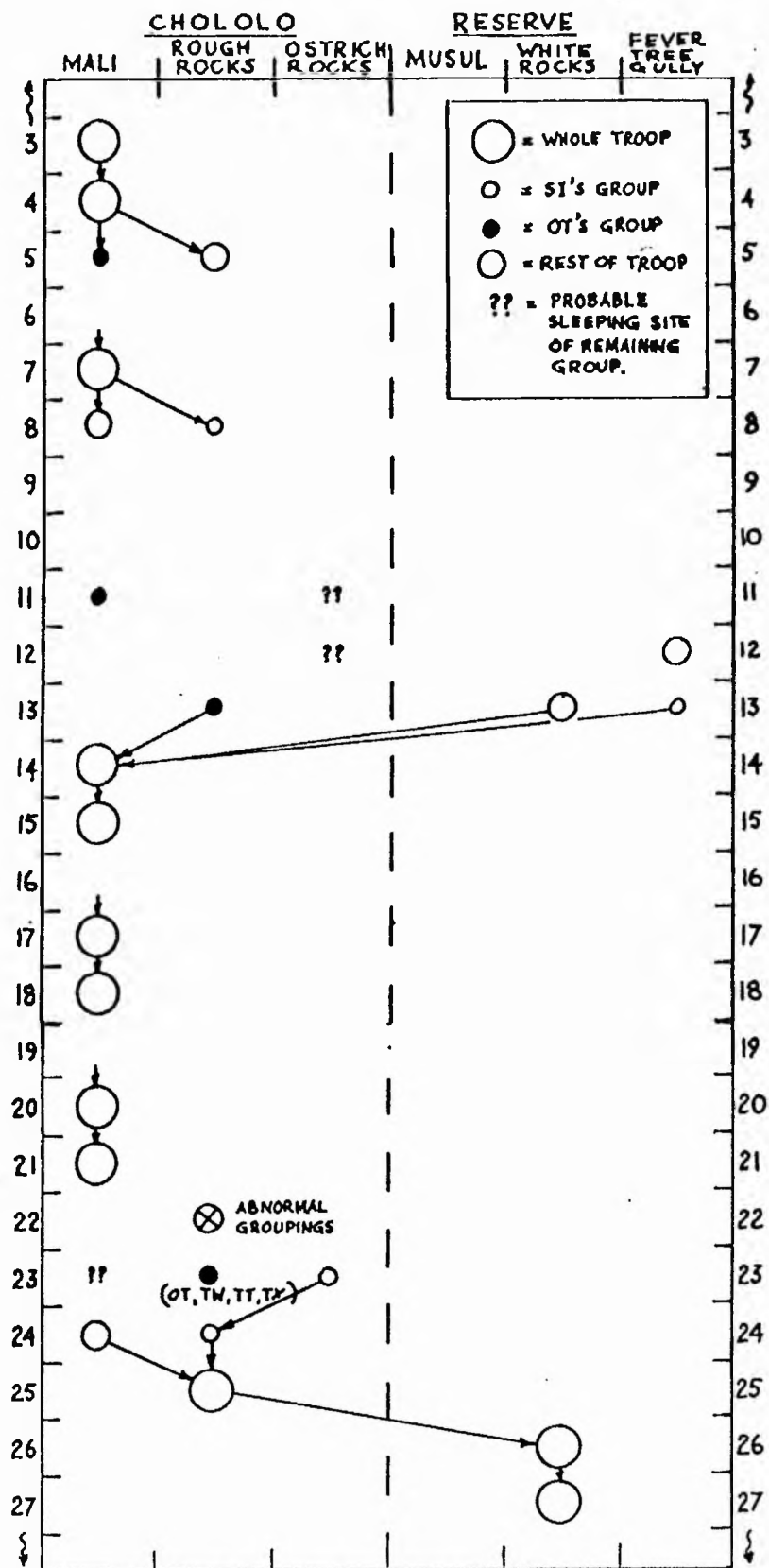


Figure 4.10(b): Fission/fusion of STT troop: sites at which the troop slept together and as separate sub-troops during October 1990.

when there was an abundant resource of *Acacia* flowers to be harvested in a restricted area, the troop in fact slept together.

Part of this sub-trooping behaviour observed in STT may relate to individual males' behaviour (Nash, 1976). Long-term demographic and ecological data from this site will hopefully be able to clarify the factors involved in this sub-trooping, and the relationship between seasonal environmental fluctuations and ranging behaviour in this on-going process.

CONCLUSIONS

This chapter has examined the behaviour of STT baboons as a whole. Day range lengths for this troop are related to biomass values. The relationship between the size of area of the home range used in a month and baboon food biomass values is complex, and is probably related to the nature of available component parts of this biomass.

The data presented here suggest that differential use of the home range may be a coping strategy for living in a seasonal environment. However, further analyses of the distribution of food resources will contribute to investigating this behaviour.

While the sub-trooping behaviour observed for this troop of baboons might be part of a process which will result in a permanent split, in this site's seasonal environment, it may alternatively be another adaptive behavioural strategy for coping with periods of resource scarcity. The combination of variation in day range length and the areas of the home range that are used, together with fission/fusion behaviour may enable this troop of baboons to survive in this seasonal environment.

In the following chapters (5 and 6) data on the behaviour of one category of individuals within this troop, namely infants and young juveniles, is presented and discussed. Data are then examined to see the effects that seasonal periods of resource scarcity experienced at this site have on the behaviour of these particular individuals (Chapter 7).

CHAPTER 5: DEVELOPMENTAL CHANGE IN THE RELATIONSHIP BETWEEN YOUNG INDIVIDUALS AND THEIR MOTHERS

INTRODUCTION

Changes during development are both physical and behavioural. During their first year of life, young baboons exhibit noticeable changes in their physical characteristics. They lose their natal black hair colouration and pink skin, and pass through a 'transitional' period to become adult-like brown/yellow haired and grey skinned by around 10 months of age (yellow baboons: Altmann et al., 1977, 1981; olive baboons: Ransom and Rowell, 1972; Nicolson, 1982). Growth and increase in weight have been well documented for *Papio* species with data from captive environments (Snow, 1967 referred to in Zullinger et al., 1984; Roberts et al., 1985; Glassman and Coelho, 1988) and from the field when there have been suitable opportunities (Berger, 1972; Nicolson, 1982; Eley et al., 1989). Growth may appear to be fairly linear in the first year (Nicolson, 1982), and the same is true for female weanlings when examined separately (Glassman and Coelho, 1988); however, Zullinger et al. (1984) have shown that like most mammals, growth data from *Papio* species fit well to the shape of a sigmoid function (Zullinger et al., 1984: Table 3).

Behaviourally, during infancy and the juvenile period individuals change from being completely dependent on their mothers for nutrition, protection, and transportation, to being independent and self-sufficient. The relationship between mothers and their offspring therefore comprises an important part of the behavioural ecology of young baboons and has been the focus of much research: Ransom and Rowell (1972), Nash (1978), Altmann (1980), Nicolson (1982) and Rhine et al. (1984) have documented many of the aspects of this relationship. When an infant is born, it is usually immediately able to cling to its mother's ventrum and to suckle for milk, though on some occasions it may be necessary, especially in the first few days, for the mother to support the infant, for example holding it to her ventrum while travelling quickly.

Constant contact with the mother gradually gives way to contact which is punctuated with periods of separation as the infant becomes more alert and interested in its social and physical environment. Infant acquisition of independence therefore involves becoming weaned from maternal milk, becoming self-mobile and being able to spend longer periods of time out of contact from the mother, and becoming an independent interactant within the troop and the surrounding environment.

Most research relating to this has been limited to the behaviour of mothers and infants, particularly in the first year of life (see references above). Because the focus of this study is the behaviour of young individuals who have just become weaned but who are still particularly vulnerable, I examine the relationship between older infants and young juveniles (up to 45 months old) with their mothers, in addition to the behaviour of younger infants.

In the following sections I present data on behaviour associated with the relationship between young baboons and their mothers during and after weaning, namely the amount of time spent suckling, in contact with the mother and in close proximity to her, and on individual differences in the time spent in contact with the mother. Chapter 6 will present data on the behavioural activities of these individuals: thus together, the present chapter and Chapter 6 describe in detail the behaviour of this age group. This provides the context for examining the effect of seasonal periods of food scarcity on behaviour (Chapter 7).

ADDITIONAL NOTES ON METHODOLOGY

The methods of focal data collection used in this study are described in detail in Chapter 2. However, the following section elaborates on a few aspects with respect to this and the following chapter.

This is not a study of infant behaviour from birth. Because interest during this research focused on the interaction of young individuals with their environment, data were collected on subjects when they became 3 months of age, already showing some

behaviour independent from their mothers. Therefore, from the data described in the following sections, only very limited inferences can be made about the behaviour of infants younger than 3 months of age. Personal, non-quantitative observations of baboons younger than 3 months old and published data from other studies can contribute to the interpretation of the age related behavioural change presented here, but effectively this chapter will describe the observed behaviour of subjects between the ages of 3 and 43 months (45 months for activity budget behavioural categories: Chapter 6).

Further, this research is not a study tracing development per se: rather it is an examination of the behaviour of individuals of certain age groups within the context of their physical environment. To this end, subjects were selected as described in Chapter 2 to represent young infants, older infants and young juveniles. Because of the distribution of available subjects within the appropriate age range, there resulted an artificial gap between 20 and 28 months of age (20 to 30 months for activity budget behavioural categories) for which no data could be collected (and also a smaller gap at 35 - 36 months old for activity budget behavioural categories): see Figure 2.5 in Chapter 2. In the figures which present mean data by age in this and the following chapter, the ages for which there are no data are left blank to clarify the presentation. Future studies involving the interaction of environmental effects with the behaviour of individuals during this period in their lives would benefit from including data from each age if at all possible, so that continuous descriptions of changes in behaviour can be made.

I must also stress that these data do not represent a longitudinal study of the same individuals over the period of 3 - 45 months. Each of the subjects studied was observed with respect to the contact behavioural categories for 7 months and with respect to the activity budget behavioural categories for 4 - 5 months (see Chapter 2 and Appendix A for description of categories), a similar approach to that of Rhine et al. (1984). Because the subjects were of different ages during the study period, they therefore do not all contribute data to each age mean. In the case of the activity budget

behavioural data, for some months there are only two individuals contributing to the mean value because of the distribution of subject ages, though there are some ages for which 6 or 7 individuals contribute to the mean. This can be seen in Figure 5.1 which presents the data from each individual for the behavioural category 'moving' from 3 to 45 months old (analysed in Chapter 6), and in Figure 5.10(a) for time spent in contact with the mother, though these are data for only infants. At some ages, only one individual was studied (i.e. for behavioural activities at the age of 30 - 34 months old with the subject TZ, and at 37 and 44 - 45 months old when EN and BE respectively were the only subjects of that age: for contact behavioural categories only one individual was studied at 19 months old (EI), 28 - 34 months old (TZ), 35 months old (EN), 36 months old (TC) and 43 months old (NR)). Such values must be regarded with due caution. Further long-term research would ideally involve the study of the same individuals continuously over a period of 36+ months to provide more complete data and with each individual contributing data to each monthly mean.

Baboons in this troop do not exhibit a birth season, so there is no regular synchrony of development with the environmental annual cycle¹. Periods in the cycle coincide with different stages in individuals' lives. However, an individual's personal development is confounded with the progression of months through the year i.e. the month of August for an infant aged 11 months old followed by the month of September means not only that the infant is a month older, now the age of 12 months old, but also that the environment has coincidentally proceeded in its annual cycle. However, for most ages, there exist data from different times of the year. Taking an average value for a behavioural frequency across these individuals at a particular age dilutes the potential effect of the environment. Details of the number of subjects which contribute to each mean value, and months for which data were collected for each age are presented in Table 5.1. Ideally, in order to look at development, data should be

¹ In the past however, when severe environmental conditions have resulted in the death of a number of infants, mothers have resumed cycling in synchrony, which has resulted in a cohort of youngsters born at about the same time.

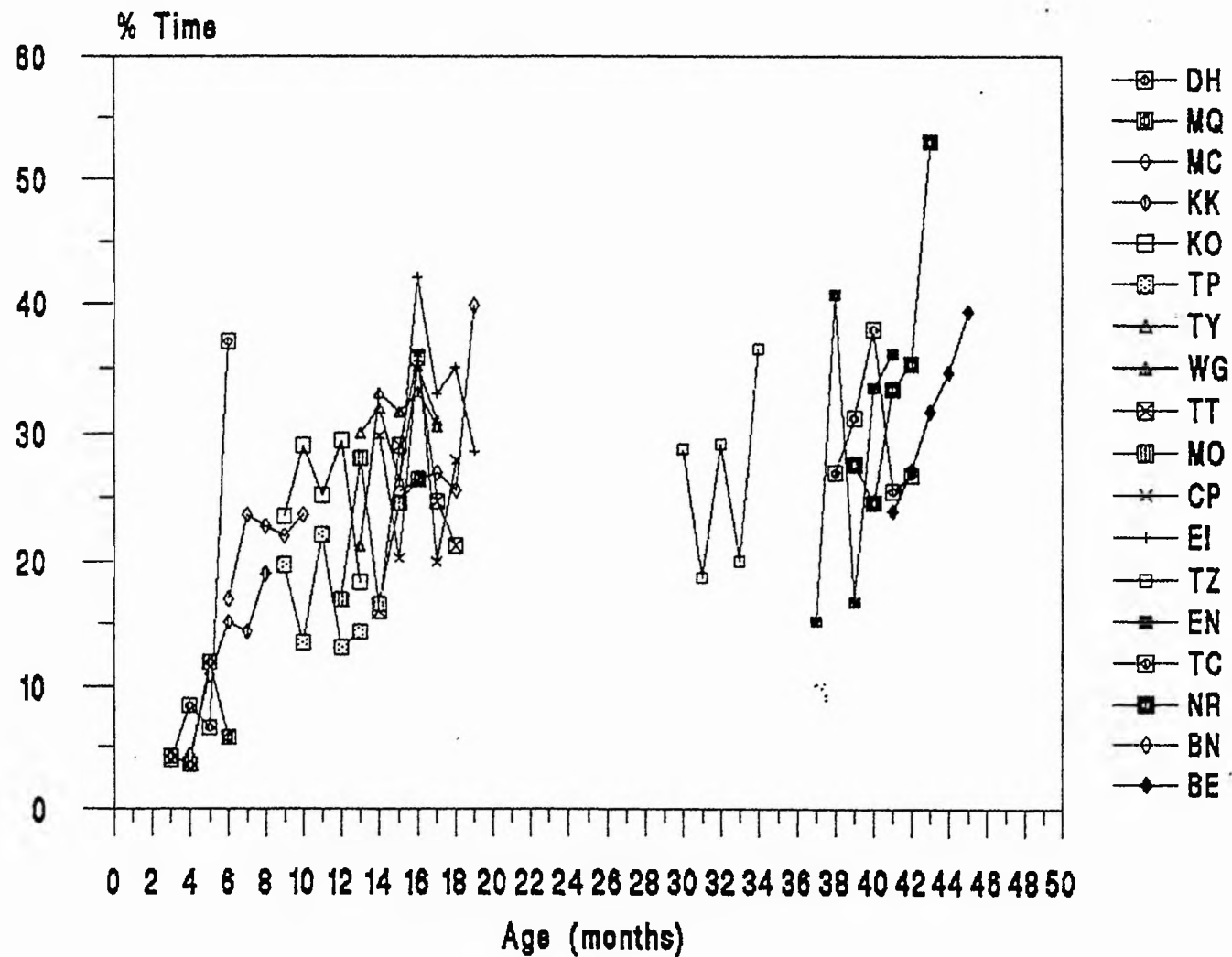


Figure 5.1: Individual data for the behavioural activity 'moving'

Table 5.1: The number of subjects and the months for which data were collected for each age: the individuals studied are denoted by their ID codes; IDs in parentheses indicate that data were recorded for contact/proximity categories only; square brackets, [], denote two individuals who were orphaned at the start of the study and thus were not included in the analysis of behaviour associated with the mother-infant relationship. Number in parentheses indicates the number of subjects used in the analysis of m-i relations.

AGE	N	APR	MAY/JUN	JUL	AUG	SEP	OCT
<hr/>							
3	2 (2)			DH MQ			
4	3 (4) (MC)		KK		DH MQ		
5	3 (3)			KK		DH MQ	
6	4 (4)		MC		KK		DH MQ
7	2 (4) (KO) (TP)			MC		KK	
8	2 (2)				MC		KK
9	3 (3)		KO TP			MC	
10	3 (4) (MO)			KO TP			MC
11	2 (4) (TY) (WG)				KO TP		
12	3 (5) (TT) (NP)	MO				KO TP	
13	5 (6) (EI)	TY WG		MO			KO TP
14	6 (6)	TT NP CP	TY WG	MO			
15	7 (6)	EI [BN]	TT CP	TY WG	MO		
16	7 (6)		EI [BN]	TT CP	TY WG	MO	
17	6 (5)			EI [BN]	TT CP	TY WG	
18	4 (3)				EI [BN]	TT CP	
19	2 (1)					EI [BN]	
<hr/>							
28	0 (1) (TZ)						
29	- -						
30	1 (1)		TZ				
31	1 (1)			TZ			
32	1 (1)				TZ		
33	1 (1)					TZ	
34	1 (1)						TZ
35	0 (1) (EN)						
36	0 (1) (TC)						
37	1 (2) (NR)	EN					
38	2 (2)	TC	EN				
39	3 (3)	NR	TC	EN			
40	3 (3)		NR	TC	EN		
41	4 (3)	[BE]		NR	TC	EN	
42	3 (2)		[BE]		NR	TC	
43	2 (1)			[BE]		NR	
44	1 (0)				[BE]		
45	1 (0)					[BE]	

collected over consecutive years or multiple seasons to minimise the variance due to environmental factors. During the interpretation of the data presented below, I take care to be aware of this potential variation in the mean values, and to therefore draw attention to specific patterns in the data only when the number of subjects implies the result is likely to be robust. The data from subject TZ particularly illustrate this point: she was the only individual available to study aged between 30 - 34 months old.

WEANING, CONTACT WITH AND PROXIMITY TO THE MOTHER

In this section, data are first presented separately for each of these aspects of the behaviour associated with the relationship between young baboons and their mothers, and then discussed together at the end of the section.

Time spent at the nipple and the process of weaning:

Time spent at the mother's nipple includes both time spent actually on the nipple where the nipple could be seen in the infant's mouth, and time when the infant was in a position where suckling on the mother's nipples was likely (see Appendix A for definitions). Time spent at the nipple may have been for non-nutritional purposes such as comfort, but since milk is usually produced in response to suckling and pulling on the nipple, it was considered appropriate not to differentiate these possible different functions. Figure 5.2 presents by age (in months) the mean percentage of time infant and young juvenile subjects spent at the mother's nipple.

At 3 months of age the mean percentage of time spent at the mother's nipple was 32.1% (SE = 5.2). The percentage of time at the nipple then declined steeply with increasing age. By 6 months of age, a mean value of 6.7% time was spent at the nipple (SE = 2.3), and at 12 months of age the mean value was 1.8% of time (SE = 0.9). The age at which the last record of time spent at the nipple was made varied across individuals: one subject (TT) was never recorded as being at the nipple from 14 - 18 months of age. The oldest age at which time spent at the mother's nipple was

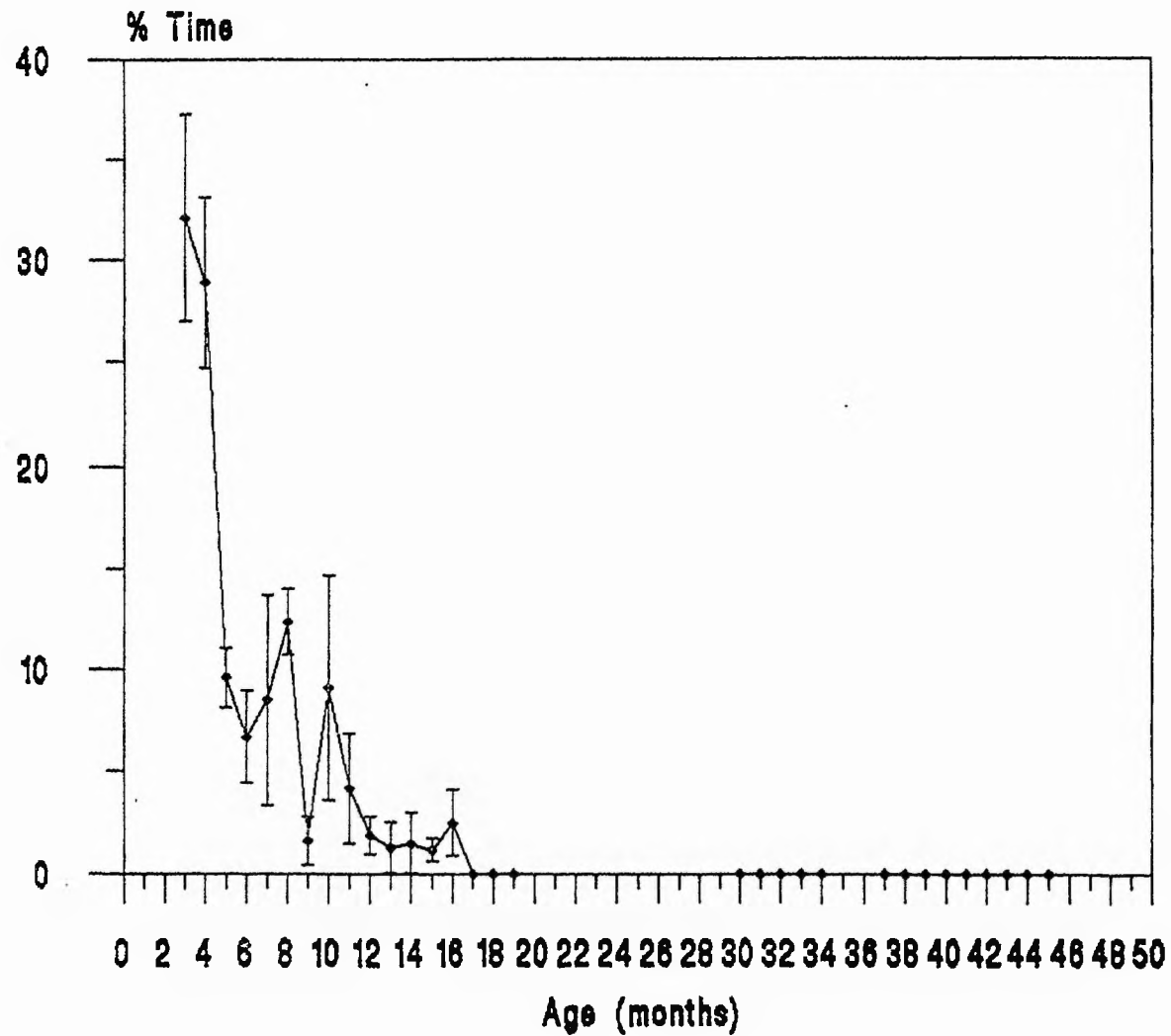


Figure 5.2: Mean percentage of time spent by infants and young juveniles (3 - 45 months old) at the mother's nipple. The number of subjects contributing to the mean at each age is detailed in Table 5.1. Error bars are standard errors.

recorded for any individual was 17 months of age (WG: 0.06%). By 18 months therefore, all the subjects in this study were no longer dependent on their mothers for nutrition.

A similar decline for time suckling from 70% in the first 8 weeks to 0% by 56 - 64 weeks old was reported by Nicolson (1982). She observed infants of 3 months of age spending slightly more than 40% of time at the nipple (Nicolson, 1982: Figure 5) which is slightly higher than the value of 32% presented here, but is consistent with it. Nash (1978) reports a decline in the amount of time infants spent on the nipple throughout the first year, but in contrast with this study where the largest drop in time spent at the nipple was at 5 months old, she reports the most marked drop between 10 - 12 months. She also stresses the individual variation in the age that infants were last seen on their mother's nipples.

During the process of weaning infants attempted to gain access to the nipple, for example slipping down towards the nipple from a dorsal riding position (pers. obs.), but were actively rebuffed by the mother, the nipple being physically blocked with her body or her moving away. Rejection by the mother was sometimes forceful, for example the infant being bitten or hit away, and the reaction of the infant could be extreme, as is illustrated by Figure 5.3 where EUSI (brown infant, 13 months old) has just been struck by his mother as he attempted to reach for her nipple and is now sitting near an adult male friend, screaming relentlessly. Appendix E contains an extract from my ad lib. notes describing such a weaning tantrum in detail, which further illustrates the response to such rejection: the tantrum lasted nearly 20 minutes, and subject EI (10 month old infant) persistently followed his mother, getting close to her and attempting to touch her nipple, despite being ignored or even attacked by her.

Figure 5.4 presents by age (in months) data on the occurrence of subjects' rejection behaviour i.e. the mean percentage of time spent in tantrums, moaning, and being rejected by the mother, whether forcefully or subtly (see Appendix A for definitions). From at least 3 months of age, subjects suffered maternal rejection. The highest mean value for percentage of time being rejected occurred at 7 months old



Figure 5.3: Weaning tantrum: EUSI, a 13 month old brown infant, having just been struck by his mother as he attempted to reach for her nipple, is now sitting and screaming relentlessly.

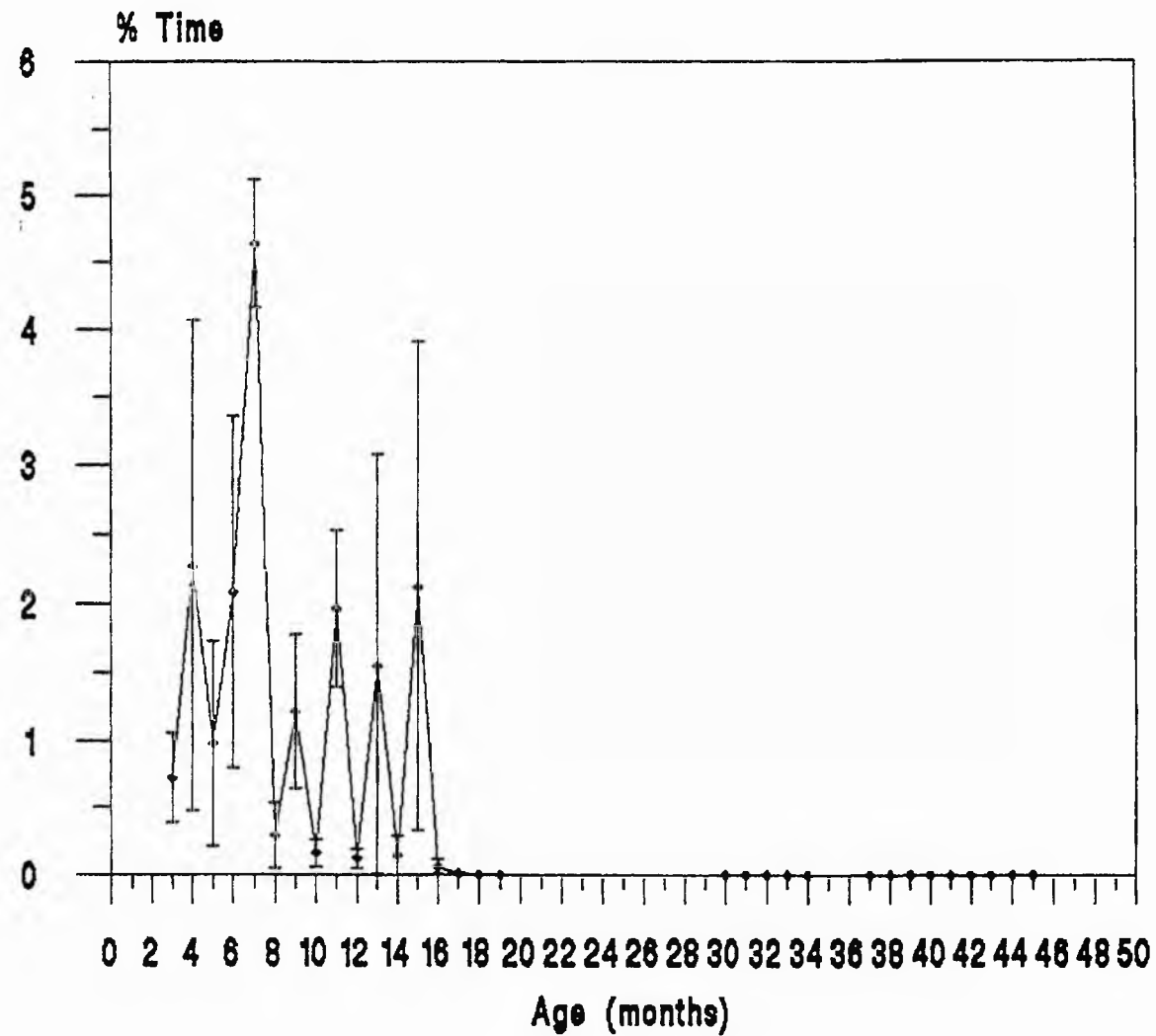


Figure 5.4: Mean percentage of time spent in tantrums, moaning and being rejected by the mother by infants and by young juveniles (3 - 45 months old). The number of subjects contributing to the mean at each age is detailed in Table 5.1. Error bars are standard errors.

(4.6%, SE = 0.5). Rejection continued to occur for subjects though with much individual variation up until the age of 17 months old (\bar{x} = 0.01%, N = 5). There did not appear to be the same clear decline in the mean values for time spent being rejected as described for mean time spent at the nipple. However, from 17 months, no bouts of rejection were observed for any individual.

The peak in rejection in the data presented here is consistent with the peak in unsuccessful attempts to suckle found by Nicolson (1982) between 25 and 32 weeks (6 - 8 months) of age. Nash (1978) reports that frequency of rejection peaked for several infants between 6 - 10 months. Ransom and Rowell (1972) found that maternal rejection varied individually, some mothers not beginning to reject their infants until they were 9 - 10 months old although others rejected their infants in the second month.

The oldest age at which an infant was recorded being rejected from its mother coincides exactly with the age of the last recorded time spent at the nipple (17 months). It seems that beyond this age infants no longer attempted to get access to their mothers' milk, and thus no longer elicited rejection.

Time spent in contact with the mother:

The mean percentage of time infant and young juvenile subjects spent in contact with the mother is presented by age (in months) in Figure 5.5. Time spent 'in contact' is the sum of the two mutually exclusive contact categories, 'ventral' and 'other' contact (see Appendix A), which cover all contact with the mother. (This is slightly different from the combined categories of 'ventral' and 'dorsal' contact used by Nicolson (1982) which omit some forms of contact. My category of 'other' contact includes dorsal riding.)

At 3 months old, infants spent a mean value of 60.3% of time in contact with the mother (SE = 4.3). This declined to 11.7% (SE = 6.1) by 12 months of age. For infants older than 12 months, the mean values dropped to about 3 - 4%. Juveniles in their 3rd and 4th years of age still maintained some contact with their mothers: the mean amount of time spent in contact over 39 - 41 months of age (where N \geq 3) was

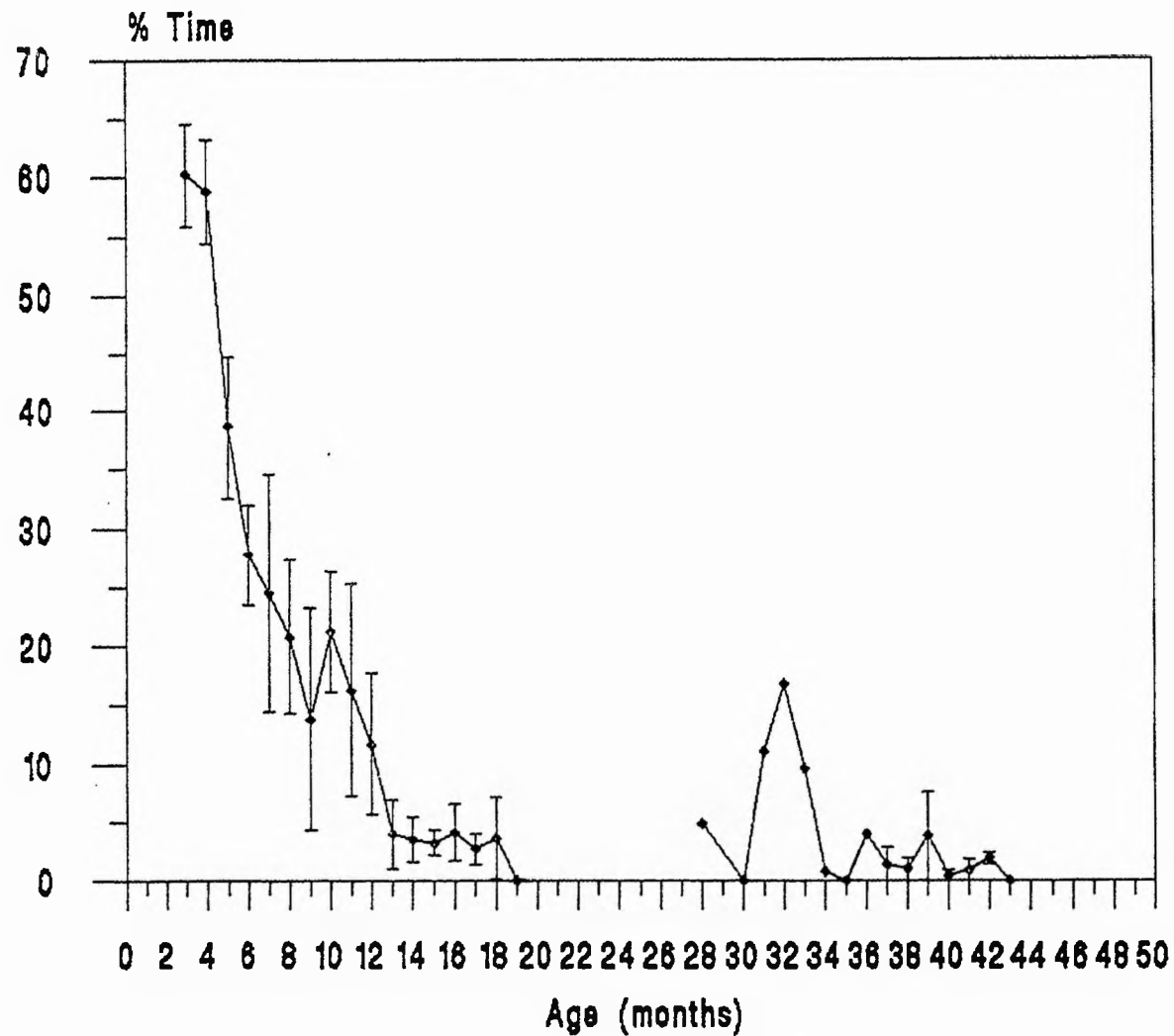


Figure 5.5: Mean percentage of time spent by infants and young juveniles (3 - 43 months old) in contact with the mother. The number of subjects contributing to the mean at each age is detailed in Table 5.1. Error bars are standard errors.

1.7%. (N.B. The data in Figure 5.5 for ages 28 - 34 months are from only one individual (subject TZ) so, as mentioned above, no interpretation of these data are attempted here or below.) The data in Figure 5.5 clearly show that there was a significant developmental change in the amount of time spent in contact with the mother as age increased, with older infants and juveniles spending less time in contact than younger infants.

The data in Figure 5.5 are similar to those presented by Altmann (1980) and Nicolson (1982). Altmann and Nicolson studied infants in the first 12 and 18 months of life respectively, and report that infants younger than 3 months of age spent very high proportions of their time in contact with their mothers, around 95% and 85% respectively (values taken from graphs: Altmann (1980), Figure 47 and Nicolson (1982), Figures 16 & 17). By three months old, infants still spent about 70% of their time in contact with their mothers in Altmann's study, and about 60% of their time in Nicolson's study. For subjects older than 18 months however, there are no comparable data for time spent in contact with the mother.

Time spent in contact with the mother therefore decreased as individuals became older, but also the nature of this contact changed. To examine this, data on time spent in contact with the mother are presented separately for time spent in 'ventral' contact (Figure 5.6(a)) and in 'other' contact (Figure 5.6(b)).

Figure 5.6(a) shows that the percentage of time spent in 'ventral' contact decreased steeply from 3 to 6 months of age, and then more slowly, until it ceased for all infants by 17 months of age. The mean values for time spent in 'ventral' contact were particularly low at 6 and 9 months of age followed by periods when time spent in ventral contact was higher. Figure 5.6(b) shows that being in 'other' contact with the mother reached its highest mean value (36.1%; SE = 4.3) at 4 months of age. Thereafter, the percentage of time spent in 'other' contact declined with age in a similar way to 'ventral' contact. However, in contrast with 'ventral' contact, these data show that older infants and juveniles still spent time in 'other' contact with their mothers.

Altmann et al. (1981) and Nicolson (1982) report that in their studies initially

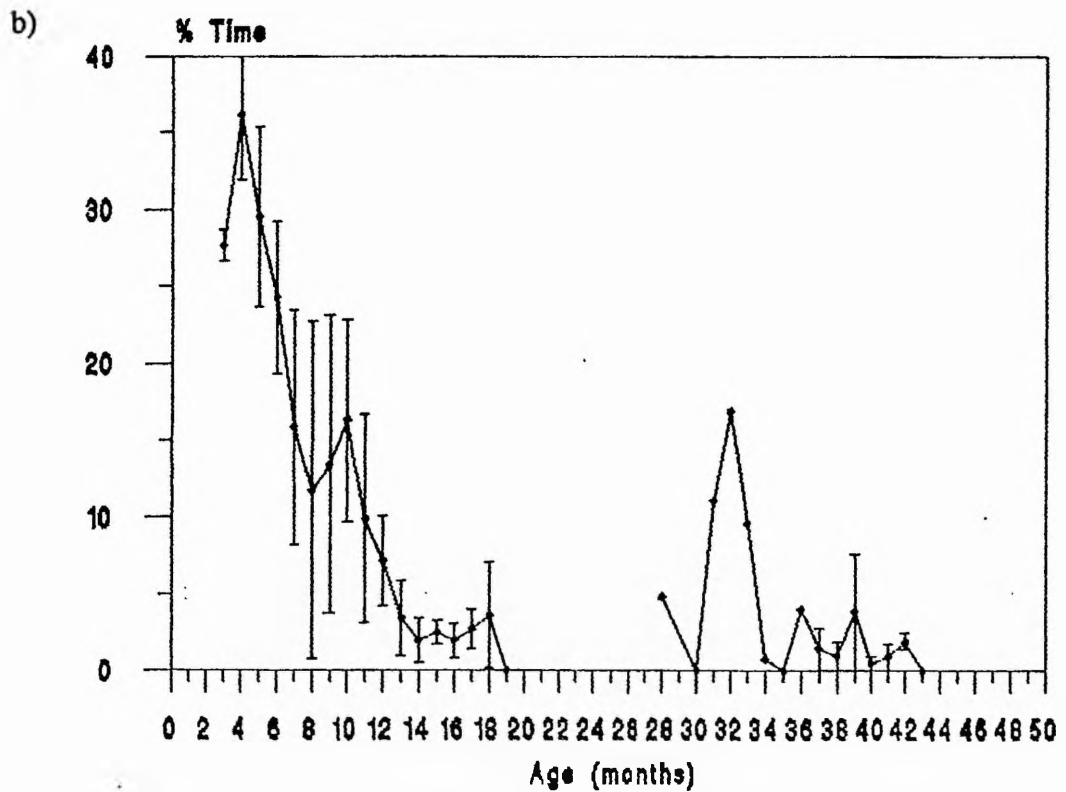
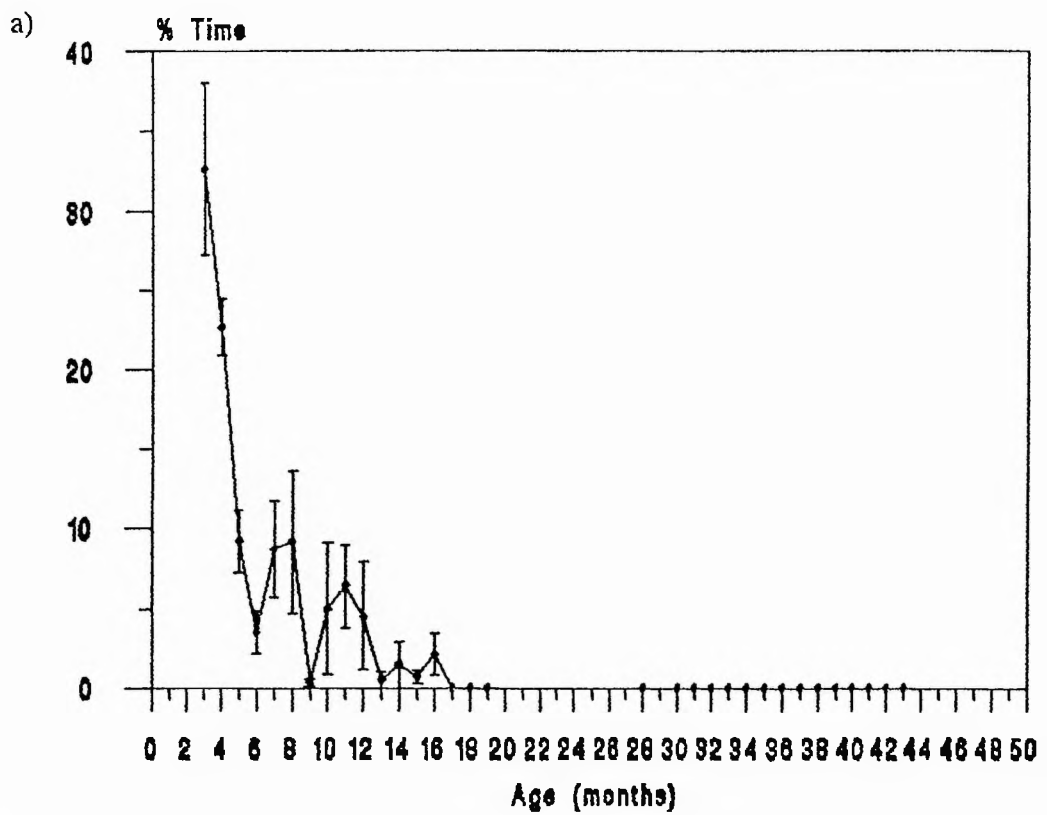


Figure 5.6: Mean percentage of time spent by infants and young juveniles (3 - 43 months old) in a) 'ventral' and b) 'other' contact with the mother. The number of subjects contributing to the mean at each age is detailed in Table 5.1. Error bars are standard errors.

contact was predominantly 'ventral' but by 8 weeks of age infants started to ride dorsally. Rhine et al. (1984) report that in the first couple of weeks of life ventral riding accounted for virtually 100% of observations but this decreased over the first year. Values for dorsal riding were initially approximately 0% of observations, increased to a plateau value of about 30% of observations between 3.5 and 6.5 months, and then decreased again, so that all riding was over by the time infants were 12 months old (Rhine et al., 1984: Figure 2).

Because the data in this study are for subjects 3 months of age and older, the behavioural patterns for young infants, the first appearance of dorsal riding and of contact with the mother other than ventral contact, at around 2 months old, are essentially missing. However, the peak in 'other contact' (Figure 5.6(b)) corresponds with the period of highest percentage of dorsal riding observed by Rhine et al. (1984), but in contrast with Rhine et al. the data presented here do not show a plateau over several months for the amount of time spent in other contact. It is likely that in Rhine et al.'s study, the plateau is due to variation in the timing of individuals' peak values for dorsal riding, which emphasises the importance of studying individual differences in behaviour (see next section).

Previous studies of the mother-infant relationship (Nicolson, 1982; Rhine et al., 1984), have shown that the highest values for the percentage of time spent in 'ventral' contact is for infants in their first month, and the highest values for 'other'/dorsal contact is, as shown here, for infants 4-6 months old. Although for this study there are no data for ages younger than 3 months old, the data in Figures 5.6(a) and 5.6(b) indicate that there is a lag of 2 - 3 months between the amount of time spent in 'ventral' contact and that spent in 'other' contact, which is consistent with these reports.

Data for percentage of time spent in ventral contact with the mother are very similar to those for the percentage of time spent at the nipple. It might be expected that ventral contact with the mother could continue beyond the last age that infants were observed at the nipple, but with my data, the correspondence between the age at which ventral contact ceased and the end of being at the nipple, is exact.

These data show that by 4 months of age, infants spent more time in 'other' contact with the mother than in 'ventral' contact. Thereafter, the percentage of time spent in 'other' contact was consistently greater than the percentage of time spent in 'ventral' contact. Nicolson (1982) suggests that ventral contact ceases and is replaced by dorsal contact by the 10th month, but in this study values for 'ventral' contact did not drop to near zero until after the end of the first year, so such 'replacement' occurred later. Comparing the behaviour of infants in two different troops, Rhine et al. (1984) note that the duration of ventral riding for infants may be affected by troop size. The timing of replacement of 'ventral' contact by 'other' contact is therefore likely to vary between populations.

There are no data on contact with the mother from previous studies to compare with these for the juvenile subjects (28 - 43 months old). As noted earlier, juveniles still maintained some contact with the mother, and this was contact other than ventral. The contact is most likely to be due to grooming interactions which still occur between the mother and her older offspring (see also Chapter 6: grooming).

Time spent out of contact but in close proximity to the mother:

The amount of time infants and young juvenile subjects spent in close proximity to the mother is presented as the percentage of time spent out of contact but within the mother's arms' reach (Figure 5.7(a)) and the percentage of time spent beyond arms' reach but within 5m of the mother (Figure 5.7(b)). These data on proximity to the mother would be more relevant if they were also compared to values for proximity of subjects to unrelated individuals in the troop, to ascertain whether time spent close to the mother is significantly different from chance proximity to, for example, any other adult female.

Figure 5.7(a) shows that the percentage of time spent within arms' reach of the mother but not in contact with her remains at about 10% for the first 7 months of age, and then drops rapidly to a level of about 3% for older infants. Juveniles 39 - 41 months old spent only a mean of 0.1% of their time ($N \geq 3$) out of contact of the

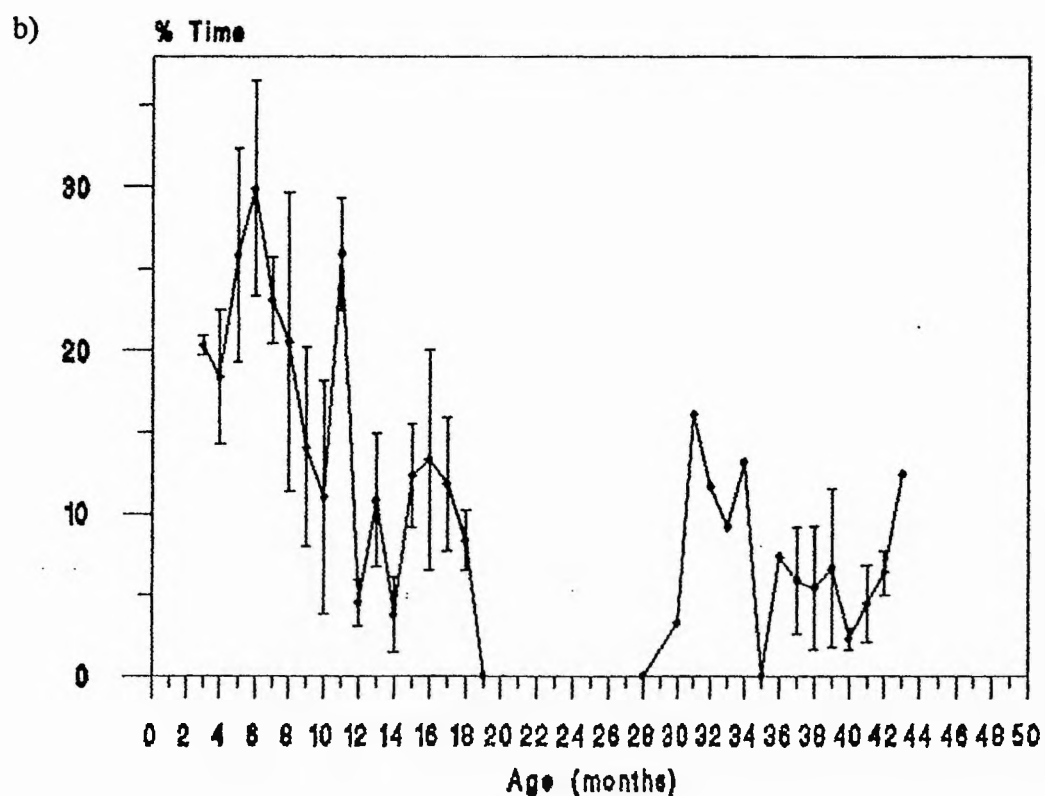
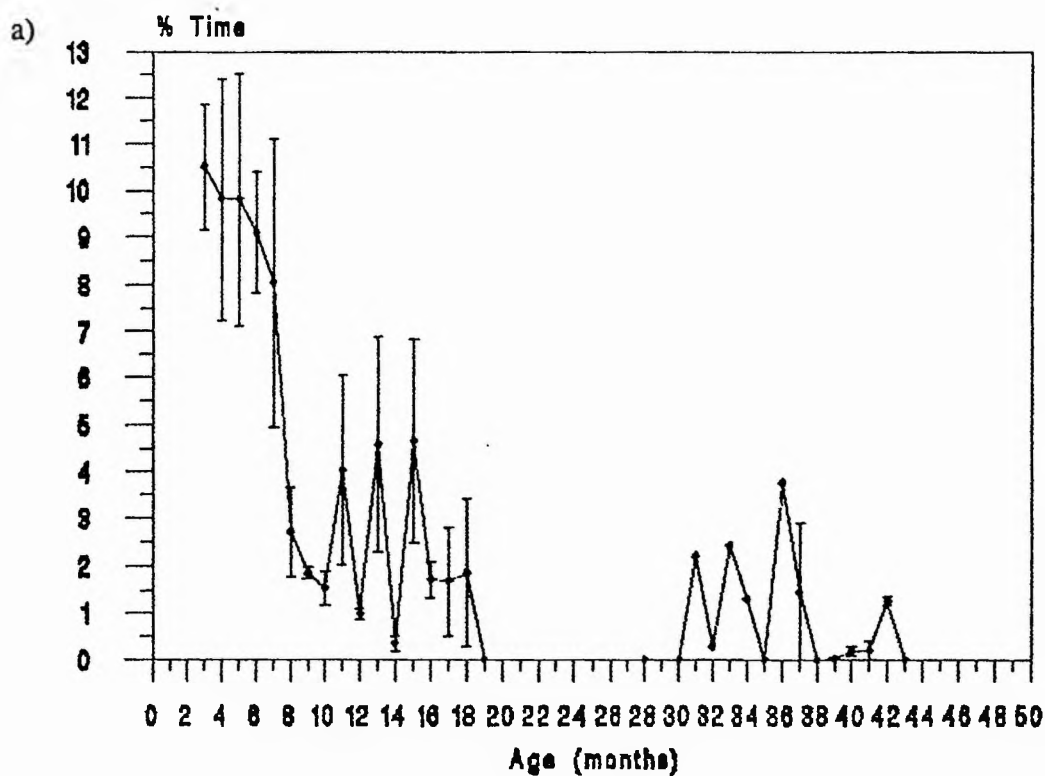


Figure 5.7: Mean percentage of time spent by infants and young juveniles (3 - 43 months old) a) out of contact but within the mother's arms reach, and b) beyond arms reach but within 5m of the mother. The number of subjects contributing to the mean at each age is detailed in Table 5.1. Error bars are standard errors.

mother but within arms' reach.

Figure 5.7(b) shows a peak mean value for percentage of time spent in the area of beyond arms' reach but closer than 5m to the mother at 6 months of age (29.9%, SE = 6.6). The time spent in this area then generally decreased with increasing age, though with more variance in the values than for other proximity measures. By the second year of life, about 10% of time was spent in this proximity category. Juveniles 39 - 41 months old ($N \geq 3$) spent an average of 4.5% of time beyond arms' reach but within 5m of the mother.

Figure 5.7(a) indicates that spending time in very close proximity to the mother (within arms' reach) though out of contact with her mainly occurred during the first half of the first year of life, perhaps during the period when the infant was starting to spend time exploring its environment (see also Chapter 6).

The values for percentage of time spent beyond arms' reach of the mother but within 5m of her show a lag behind those for contact with the mother similar to the 2 - 3 months lag found between other and ventral contact (see previous section).

Sex differences in grooming relationships with the mother for immatures have been found in other studies (e.g. Pereira, 1984) (see Chapter 6). Since young juveniles of around 40 months of age still spent about 5% of their time beyond arms' reach but within 5m of the mother (in addition to the maintained time in contact - see earlier), it would be interesting to test whether such sex differences exist in measures of proximity to the mother: female offspring might continue to maintain these levels of proximity throughout their lives, but juvenile males who prepare to leave their natal troop as they get older, may exhibit different patterns of behaviour (for example, increased levels after they have been away from the troop for a few days). In this study, there are insufficient data to be able to test for such differences between the behaviour of young males and females.

Presenting these data cumulatively (Figure 5.8) shows more clearly the overall percentage of time spent in close proximity to the mother (including in contact) and how this changed with increasing age. At 3 months of age, a mean value of 91.1%

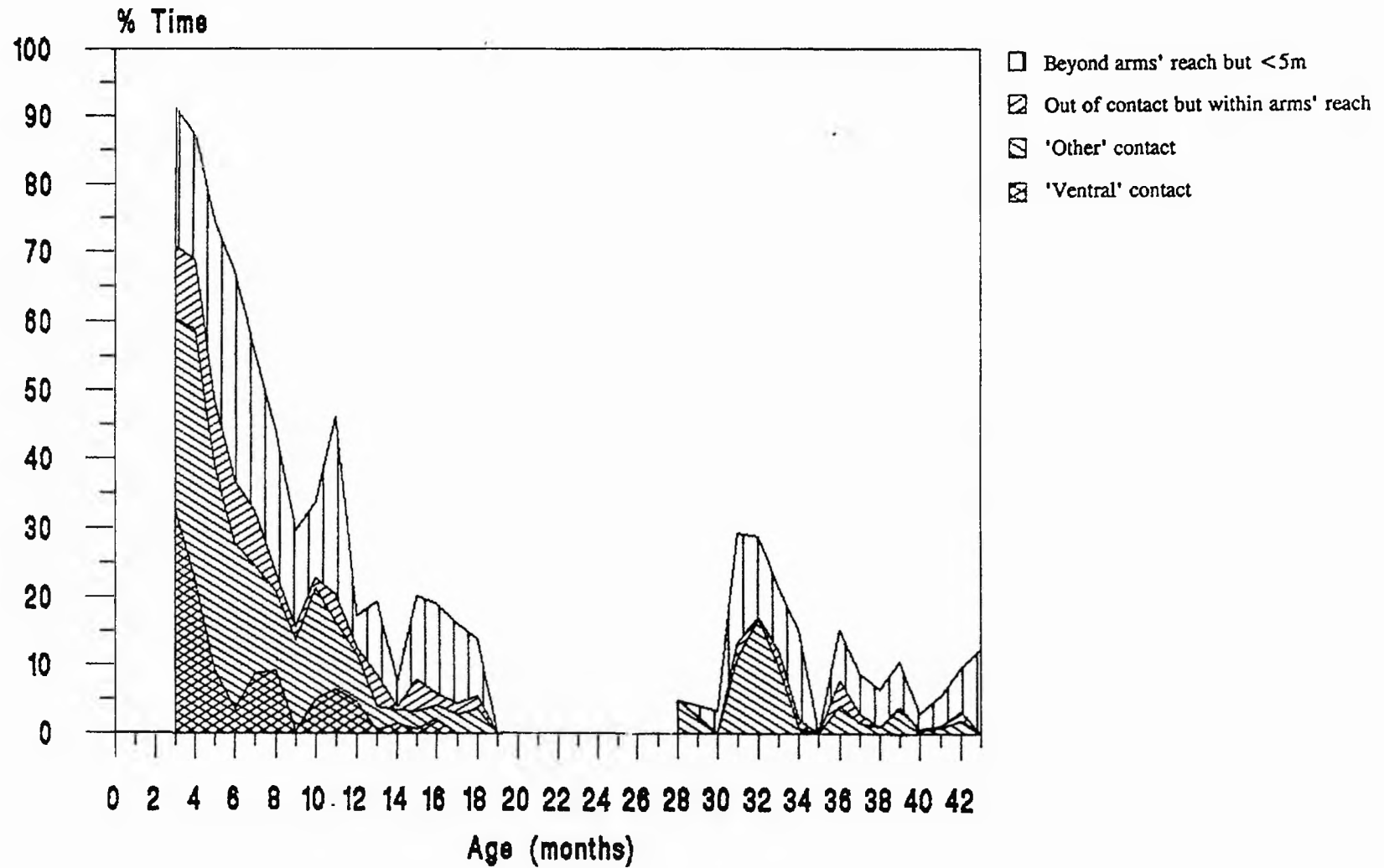


Figure 5.8: Mean percentage of time spent in ventral contact with the mother, other contact with the mother, out of contact but within arms' reach of the mother, and beyond arms' reach but within 5m of the mother, presented cummulatively.

time was spent within 5m of the mother. These data show a general decrease in the percentage of time spent within 5m of the mother to a value of 17.2% by the age of 12 months old. Values of 10 - 20% were still maintained by juvenile subjects aged 34 - 45 months old. The obvious correlate of these changes is that the percentage of time spent further than 5m away from the mother increases with increasing age, and in the second year of their lives and beyond, young baboons may be spending as much as 85% of their time more than 5m away from their mothers, and thus acting quite independently from her.

The time spent within 5m at 3 months of age in this study is comparable with the values presented by Altmann (1980) and Nicolson (1982): over 90% and about 98% respectively (values taken from graphs). The mean value for 12 months of age, at 17%, is low compared to the data presented by Altmann (> 30%) and Nicolson (approximately 40%). Nicolson's data show a decrease to about 15% for subjects aged 16 - 18 months old. At present, there are no comparable data for subjects in their 3rd and 4th years of life.

The data for ages 28 to 35 months old comes solely from subject TZ. As with the data on time spent in contact, no interpretations of these data are made, other than to note that in comparison with juveniles over 35 months old, TZ spent high percentages of time in other contact and within 5m of her mother. TZ is the sibling of TP, whose contact behaviour will be discussed in the following section because she spent a high percentage of time in contact with her mother at a late age (see section 'Individual variation in contact behaviour' below). This suggests that systematic comparison of the behaviour of consecutive siblings would be rewarding, although it would be a major task spanning several years.

Discussion:

The data presented in this section describe developmental change in the behaviour associated with the relationship between individuals and their mothers. Figure 5.9 presents a comparison of the data on mean time spent in contact with the

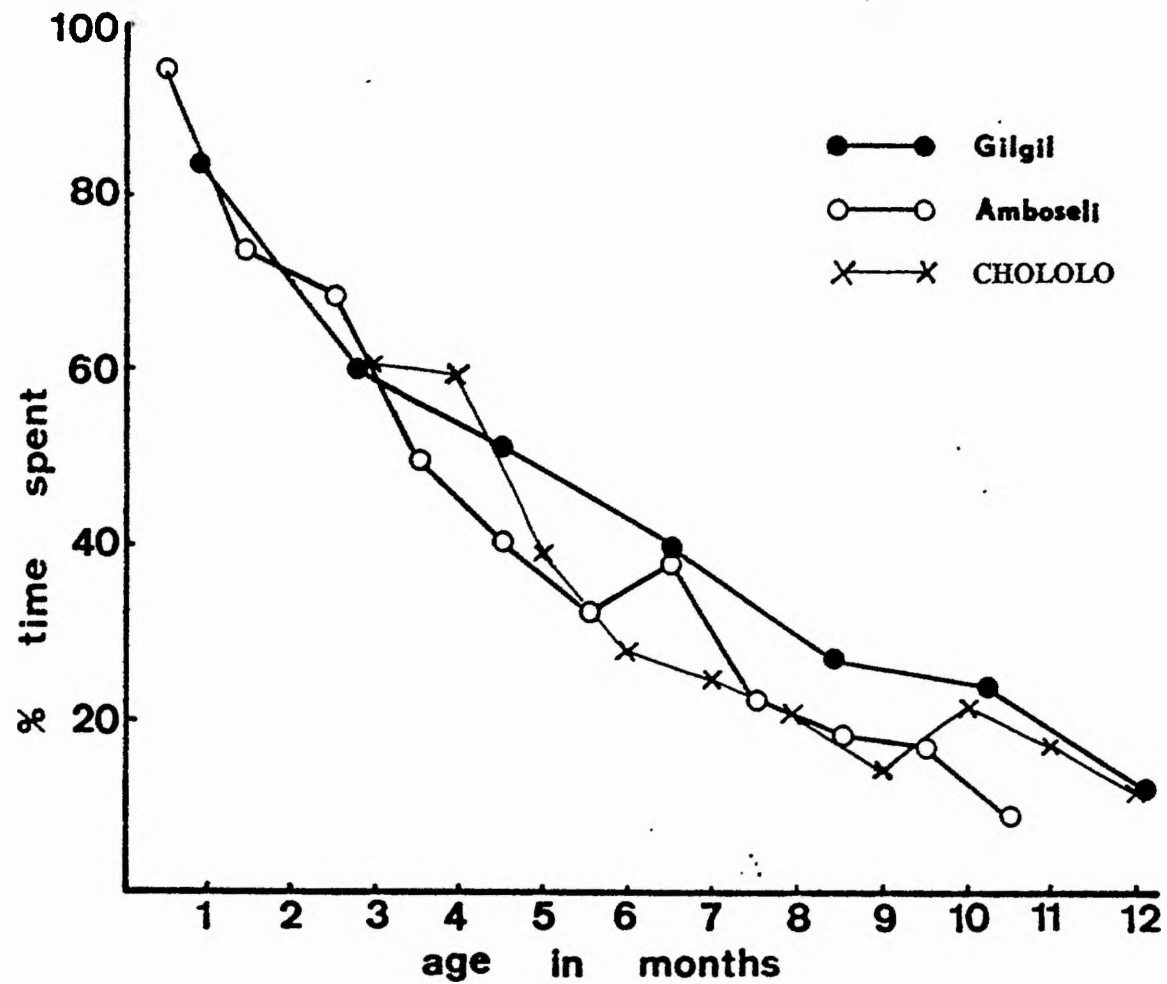


Figure 5.9: Comparison of time spent in contact at Chololo with the data from Gilgil and Amboseli taken from Nicolson, 1982: Figure 17.

mother from this study with those from the two studies which provide the most complete information on the mother-infant relationship (Altmann, 1980; Nicolson, 1982). The decline in mean time spent in contact with the mother is very similar in all three studies. This and the other comparable results mentioned in the section above are remarkable since the three studies vary widely in the amount of rainfall and environmental conditions at the sites (annual rainfall at Cholulu: 690mm (1990); Amboseli: 225mm (1975); Gilgil: 679mm (1978)), and in the size of groups studied. Developmental change in this behaviour therefore may be relatively independent of these factors within the range of the three studies, though it is likely that the mean values presented here conceal individual differences in behaviour which are a response to environmental conditions and other factors (see also next section and Chapter 7).

Weaning from maternal milk and from being transported by the mother both occur during individuals' acquisition of independence, while more time is spent feeding by the individuals on their own (see also Chapter 6). Many factors such as the energetic costs of lactation (Altmann, 1980) and of infant-carrying (Altmann and Samuels, 1992) are involved in the process of weaning and the resolution of parent-offspring conflict (Trivers, 1974; Altmann, 1980). At first it is the infant that initiates separation, but at around 2 months of age, the mother starts to initiate and reinforce separations (Altmann, 1980), and after the first few months, close proximity between mother and her offspring is largely maintained and sought by the infant (Nicolson, 1982; Nash, 1978). The data from this study have shown that some contact with and proximity to the mother is maintained even in the fourth year of life. Proximity to the mother may perhaps be still important for older infants and young juveniles who are weaned from their mother's milk and transport because of the potential to observe their mother feeding and to directly obtain discarded food resources from her or indirectly gain better access to food resources through the support she offers (Nicolson, 1987). Nicolson notes that 'whether mother or infant is more responsible for independence has become less compelling than how specific life historical, social and environmental factors can influence the costs and benefits of parental care' (1987, p333). Data on the

amount of time spent in contact with and in close proximity to the mother are examined with respect to food availability in Chapter 7.

INDIVIDUAL VARIATION IN CONTACT BEHAVIOUR

Within individual mother-offspring pairs, the data from this study show a great deal of variation in infants' acquisition of independence and their degree of attachment. Figure 5.10(a) presents the percentage of time individual infants spent in contact with their mother. (The data for individual juveniles are omitted from the diagram for clarity.) Although the mean data, presented in Figure 5.5, demonstrate a fairly regular decline in the percentage of time spent in contact, individual data did not necessarily follow a uniform schedule or pattern of behaviour. Some individuals (namely TP, MO, WG, NP) spent large percentages of time in contact with their mothers at ages older than the other subjects, for example as late as 11 and 12 months old in the cases of WG and NP. The age until which infants remained for a substantial proportion of their time in contact with their mother, and the amount of time spent in contact, showed large individual differences for many of the subjects. Such variation was similarly found in individuals' values for the other measures of proximity and weaning.

We can compare qualitatively the behaviour of pairs of subjects at the same age to illustrate these individual differences: Figure 5.10(b) presents the data for two such pairs. Subject TP (filled large square) at 7 months old spent 45.7% of time in contact with her mother, in contrast with KO (open large square) who spent 0.4% of time in contact with his mother at the same age. The data from TP exhibit a decrease in the percentage of time spent in contact, but the values by age are generally higher than those for KO. Similarly, WG (filled small square) spent more time than TY (open small square) in contact with mother, spending as much as 43.3% time in contact at 11 months of age, compared with a value of 5.3% for TY at the same age.

The data presented in Figure 5.10(a) indicate that the contact behaviour of individuals in the first 6 months of their lives did not show distinct differences: there

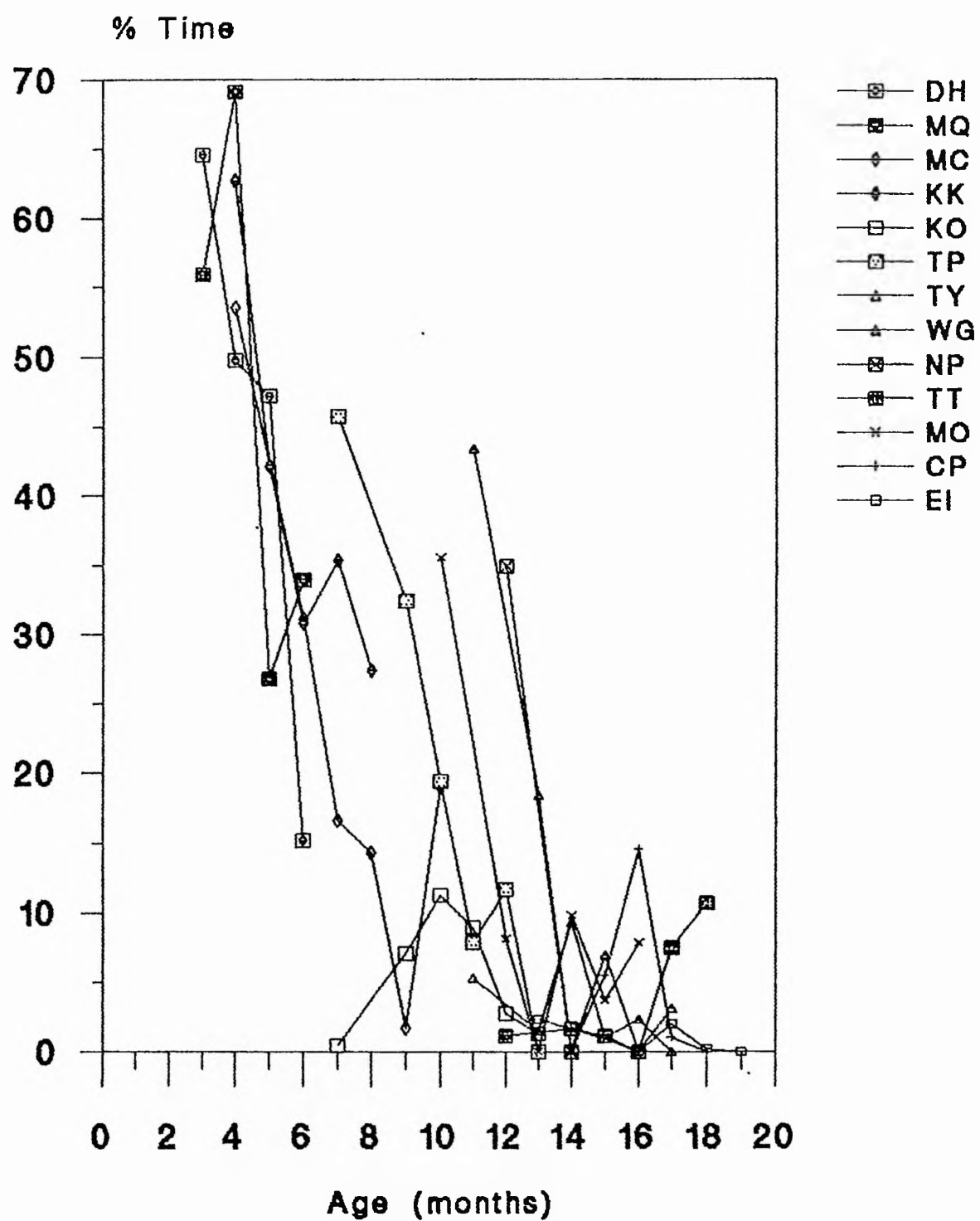


Figure 5.10(a): The percentage of time individuals infants spent in contact with the mother.

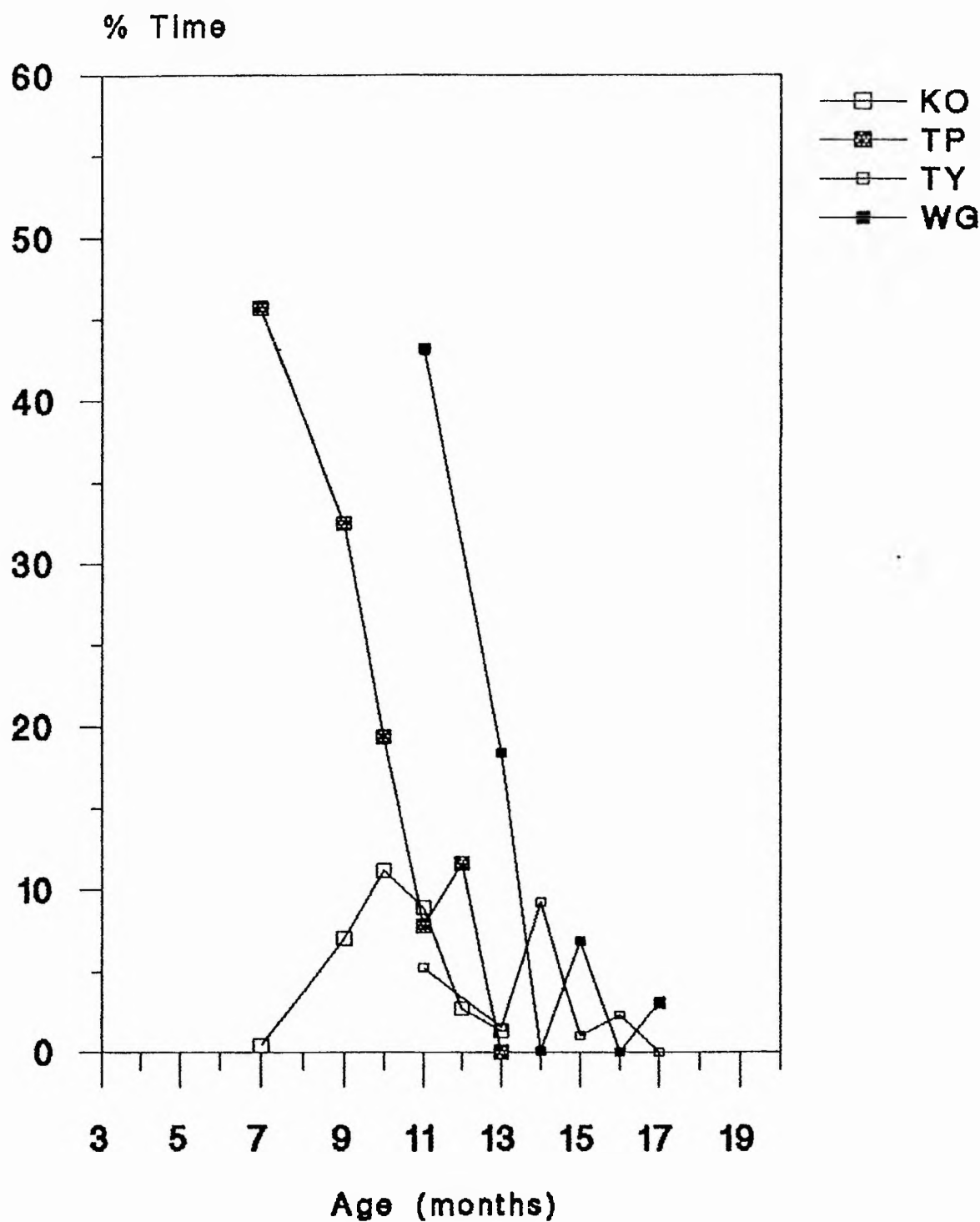


Figure 5.10(b): The percentage of time subjects paired by age spent in contact with the mother.

were greater individual differences in the percentage of time spent in contact with the mother in the second half of the first year of life. (Altmann (1980) denoted differences between the behaviour of individuals from birth, so the findings reported here may be an artifact of the limited period of data collection.) In order to examine quantitatively the behaviour of subjects at these ages where individual variation seems to be a maximum, data on the amount of time individuals from 6 to 14 months of age spent in contact with their mother are presented in Table 5.2(a). The data for some individuals show a marked decline in the amount of time spent in contact (i.e. MC, TP, MO, WG, NP) whereas others at the same ages do not (i.e. KO, TY, TT). (Higher and declining values for time spent in contact with the mother must have occurred for the latter subjects at ages for which data were not collected on those individuals in this study.) These data further illustrate the descriptive paired comparisons made earlier.

In order to examine further individual variation in the timing and amount of contact behaviour, Table 5.2(b) presents data on those individuals in this age group who exhibit a change in the amount of time spent in contact with their mothers. Two values for the percentage of time spent in contact with the mother, $>30\%$ and $<10\%$, were selected as objective criteria for discussing the change in percentage of time in contact. Individuals clearly varied in the ages between which the amount of time spent in contact decreased from $>30\%$ to $<10\%$. The number of individuals in this group is small, but data on the parity and rank of mother for these individuals show no consistent association with the ages of decline in time spent in contact. However, there does seem to be an association between sex of the individual and whether the change from a high to a lower percentage of time spent in contact with the mother occurred at an earlier or later age: of the five individuals in Table 5.2(b), the three for whom this change occurred at an earlier age were female. Although data were collected on siblings during this study (see Chapter 2) where the parity and rank of the mother would be controlled, the ages for which data were collected on the siblings were different, so such comparisons could not be made.

Nicolson (1987) notes the variation in mother-infant relationships between pairs

Table 5.2(a): Percentage of time spent in total contact with the mother by individuals between the ages of 6 and 14 months old.

ID	AGE (months)									
	6	7	8	9	10	11	12	13	14	
MC	31.2	16.6	14.3	1.7	19.0					
TP		45.7		32.5	19.4	7.8	11.6	0.0		
KO		0.4		7.0	11.2	8.9	2.7	1.3		
MO					35.5		8.1	0.0	9.8	
WG						43.4		18.4	0.1	
TY						5.3		1.5	9.3	
TT							1.2		1.7	
NP							34.9		0.0	

Table 5.2(b): Details of sex (male (m)/female (f)), and mother's parity (primiparous (p)/multiparous (m)) and rank (from Barton, 1989) for individuals in the age group of 6 - 14 months old who exhibit change in the amount of time spent in contact with their mothers. Also recorded are the ages between which the amount of time spent in contact changed from >30% to <10%.

ID	SEX	MOTHER'S		AGE (months)	
		PARITY	RANK	>30%	<10%
MC	f	m	12	6	9
TP	f	m	4	9	11
MO	f	m	9	10	12
WG	m	p	?	11 [12]*	14
NP	m	m	15	12	14

* Data are not available for WG at 12 months of age; it is possible that time spent in contact with the mother is >30% at that age.

of individuals, and discusses individual differences in frequency of rejection and the time course of infant independence in relation to characteristics of the mother. She reports that older and more experienced (multiparous) baboon females were less rejecting of their infants and spent more time in contact with and in proximity to them (Nicolson, 1982; Ransom and Rowell, 1972). Altmann (1980) denoted two types of mothers: 'restrictive' and 'laissez-faire' where infants of 'restrictive' mothers spend more time in contact with their mothers throughout at least the first half of their lives compared with infants of 'laissez-faire' mothers, and showed that the ranks of 'laissez-faire' mothers were significantly higher than those of 'restrictive' mothers. Gomendio (1990) found that in a captive colony of macaques, daughters of low ranking females suckled more frequently. Rank and maternal characteristics therefore may affect not only the percentage of time an infant spends in contact with its mother, but also the nature of its suckling patterns. However, although the effect of infant gender on mother-infant relationships has been examined systematically in field studies where enough data were available (e.g. Altmann, 1980; Nicolson, 1982), no major sex differences in behaviour have been found (Nicolson, 1987).

The data presented in this study contrast with the results described above. However, the number of subjects examined here is too small to carry out statistical analyses of the influence such factors might have on individual differences in contact behaviour. More field research which is specifically designed to examine individual differences in behaviour and the effects of various individual characteristics would be instructive.

The data presented here indicate that there are individual differences in the scheduling and amount of time that infants in this study spent in contact with their mothers. In addition to the characteristics of mothers and their offspring, environmental conditions and particularly the amount of food that is available, might also be expected to influence the timing and nature of weaning and contact behaviour. An examination of the individual differences described above with respect to biomass data and seasonally available food is made in Chapter 7.

CONCLUSIONS

The data presented in this chapter have described behavioural change in the mother-offspring relationship where time spent suckling and in close proximity to the mother decreased with age. The patterns of behaviour were comparable to those found in previous studies of young baboons. Complete nutritional weaning occurred by the age of 18 months, though after 12 months old, little time was spent at the mother's nipple. Data from this study and those from Amboseli (Altmann, 1980) and Gilgil (Nicolson, 1982) are striking in their similarity. These studies are separated temporally and spatially, and the study sites vary in their habitat and the types of food available (Strum, 1987; Altmann, 1980; pers. obs.); yet the patterns of behaviour associated with the mother-offspring relationship in the first year of life are very consistent. Change in the time spent in contact with the mother with increasing age (Figure 5.9), and the amount of time spent at the nipple and within 5m of the mother exhibit declines which are similarly scheduled at all three sites. Age by which ventral contact dropped to virtually zero and was replaced by other contact varied between two of the sites, where this change in behaviour occurred later at Chololo than at Gilgil; however, it seems likely that at a population level, the pattern of developmental change in these behaviours associated with the mother-offspring relationship may be independent of environmental conditions.

This chapter has presented data on proximity to the mother for older infants and young juveniles have been presented where few or none were previously available. These data show that about 20% of the time of individuals who are weaned is still spent within 5m of the mother. Individual differences in contact behaviour have been shown for infants aged 6 to 14 months old, though the data set was too small to examine statistically the influence of various factors on individuals' weaning behaviour.

In a seasonal environment such as that experienced at Chololo, it might be adaptive for these particularly vulnerable individuals to change the amount of time spent in close proximity to the mother and their schedule for weaning in response to periods of food scarcity. The impact of seasonal stress on these aspects of the behaviour of

young baboons will be examined in Chapter 7.

Chapter 6 first presents data on the developmental change in the behavioural activities of individuals in this age group beyond the behaviour associated with the mother-offspring relationship as a context for examining the effect of seasonality.

CHAPTER 6: DEVELOPMENTAL CHANGE IN THE BEHAVIOUR AND ACTIVITY BUDGETS OF INFANTS AND YOUNG JUVENILES

INTRODUCTION

Chapter 5 has presented data on weaning behaviour and the amount of time spent in close proximity to the mother, which describe major age-related changes in the relationship between mothers and their offspring during the first years of life. As mentioned in Chapter 1, the main focus of previous research on young baboons has been the mother-infant relationship and the development of social behaviour (see references cited in Chapter 1). There are few published studies on infant and young juvenile baboons which present quantitative data on other behavioural activities, particularly with respect to feeding ecology. Nash (1978), Nicolson (1982) and Pereira (1984; Pereira and Altmann, 1985) provide data on some categories of behaviour (feeding, moving, resting, grooming, socialising/play etc.) for subjects of this age, and Owens (1975) has studied one specific activity, that of play, for subjects up to about 3 years old. However, developmental changes in the occurrence of and time spent performing other behavioural activities have not been examined to the same extent as developmental change in the relationship between mothers and their infants. Pereira and Altmann (1985) note that 'age-dependent changes in modes of aggression, affiliation, ... foraging and travel are all important candidates for future investigation' (p285).

Apart from the work of Nicolson (1982) on infants and Pereira (1984) on juveniles, the activity budgets of infant and juvenile baboons have similarly not been comprehensively studied. The requirements of a young infant who is still suckling and those of an older infant or young juvenile who is weaned and independent from its mother are likely to be very different from each other, and from the requirements of an adult. Their behaviour is nevertheless constrained by the same time limits (i.e. the number of hours in the active day). It is therefore of particular interest to examine the

activity budgets of young baboons of different ages and to elucidate differences in how they apportion their time.

Conventionally, four main categories of behaviour are used when studying activity budgets of a species, namely feeding, moving, resting and socialising (Dunbar, 1988; Post, 1981, for the activity budgets of adults). In this study, I was particularly concerned with constructing a more detailed account of how infant and young juvenile baboons spend their time (principally to examine how this time budget was affected by seasonal periods of food scarcity - see Chapter 7). I therefore distinguished 24 behavioural categories (defined in Appendix A, and see Chapter 2 and 'Additional notes on methodology' below) to describe the behaviour of these individuals.

In this chapter, data on the behavioural activities of infants and young juveniles are presented first separately and then together as a complete activity budget, in order to examine age related change in behaviour and in how these baboons apportion their time. Differences in the behaviour of groups of young infants, older infants and young juveniles are tested statistically, but the data on behaviour and activity budgets are presented by age (in months) so that the pattern of developmental change can be described.

As with the data presented in Chapter 5, understanding developmental change in behaviour is an important prerequisite for examining the effects of seasonal fluctuations in environmental conditions on the behaviour of this age group of baboons.

ADDITIONAL NOTES ON METHODOLOGY

Description of behavioural categories:

The following mutually exclusive behavioural categories were selected to provide a comprehensive account of how young baboons spend their time. These categories are defined in Appendix A, and the method of data collection used is described in Chapter 2. The occurrence of some behaviours was extremely rare e.g.

active exploring, supplanting/being supplanted, carried by male/with male in conflict: it was considered inappropriate to analyse these data with respect to age, and descriptions of the categories are not included below. The behavioural categories 'at the nipple' and 'rejection' have already been described and discussed in Chapter 5.

Moving: This behavioural category consists of all locomotion which is pursued independently i.e. without being carried or assisted by the mother or any other member of the troop. It does not include locomotion which is involved in exploring for food, or in social or environmental exploring (see below). Pereira (1984) used a category of 'moving' which excluded climbing and arboreal locomotion, and Nicolson (1982) distinguished between climbing and walking. For this study, it was considered that time spent climbing was generally brief in duration, mainly followed by another activity (e.g. exploring for food or socially exploring etc.) to which end the climbing was just a means, and therefore could be viewed as an extension of 'moving'. However, the categories of locomotion in all three studies are nevertheless very similar, and so the data can be compared.

Exploring categories: Exploring involves behaviour where the subject interacts with its physical and social environment with the possible function of discovering the properties of these environments. Specifically, such behaviour is divided into three categories: 'environmental', 'social' and 'active' exploring. 'Environmental exploring' includes the manipulation and investigation of physical objects and potential food items, and play when alone; 'social exploring' includes play with other individuals and active social interaction or investigation, but excludes brief greetings, threats, grooming and being groomed. Figures 6.1(a) and (b) illustrate 'environmental' and 'social' exploring respectively. ('Active exploring' is defined as the simultaneous occurrence of both 'environmental' and 'social' exploring, but these categories occurred only rarely and are not analysed here.)

The category of 'social exploring' involves a number of related behaviours (see definition in Appendix A). Rather than being just the category of 'social play' for example used by Owens (1975), Nash (1978), Nicolson (1982) and Pereira (1984),



Figure 6.1(a): 'Environmental exploring': manipulation and investigation of physical objects and potential food items; play when alone.



Figure 6.1(b): 'Social exploring': play with other individuals and active social interaction or investigation.

which includes 'rough-and-tumble' and 'chasing' play behaviour, it also includes any exploratory social interactions which are longer than greetings (for example, an infant clambering over the body of an adult male who is being groomed by the infant's mother, or a juvenile trying to mount another individual). Although the category of 'social exploring' used in this study includes other behaviour in addition to that included in the 'social play' category used in other studies, data can still be broadly compared.

Distinguishing types of exploring, 'environmental exploring' and 'social exploring', is similar to categorising different forms of play described by Martin and Caro (1985) and Walters (1987) as 'social play' (equivalent to 'social exploring'), 'object play' and 'solitary locomotor play' (together probably equivalent to 'environmental exploring').

Attending categories: The categories 'attending environmental' and 'attending social' involve behaviour where the subject is inactive, but its attention is clearly focussed on a feature of the physical environment (food sample, potential predator, etc.) or a feature of the social environment (a social interaction within the troop, another individual screaming, etc.) respectively. Nicolson (1982) collected data on the occurrence of 'monitoring' (visual scanning from an elevated position), which is comparable to the behaviour described by these attending categories.

In contrast, the category 'visually attending' consists of all behaviour where the subject is inactive and looking at or watching something, but the focus of their gaze is general or unknown to the observer. This category also includes bouts of autogrooming. Within the description of 'visually attending', it is implicit that although no action or interaction involving the subject is occurring, the subject is alert and that its attention is focused on something in its environment. Therefore, in this study 'visually attending' is taken to be a distinct behavioural category, not subsumed by the category of 'resting' (as is probably the case in other studies). 'Attending environmental' and 'attending social' categories of behaviour can be viewed as the precursors of environmental and social exploring.

Resting: The behavioural activity of resting specifically refers to sleeping and resting with eyes shut. This is in comparison to the behavioural category 'visually attending' discussed above. Nicolson (1982) defines resting as 'reclining, with torso in contact with the ground', and Pereira (1984) defines resting as being when a subject is engaged in behaviour which he has not otherwise defined: both these definitions are different from the one used in this study. Data from the combined categories of 'visually attending' and 'resting' in this study are more likely to be comparable with those for 'resting' used in these other studies.

Grooming categories: The activities of grooming and being groomed are distinct social behaviours which are clearly recognisable, and which have been the focus of previous baboon field studies (e.g. Carol Saunders, pers. comm.). The activity of social grooming has the function of facilitating the removal of dirt, dead skin and ectoparasites, especially from parts of the body which are not easily reached by individuals themselves. Grooming also functions in the development and maintenance of social relations within the troop. Behavioural categories for grooming used in other studies are clearly defined and offer comparable data to those collected in this study.

Social interactions of brief duration: The behavioural categories of receiving aggression, initiating aggression, avoiding, receiving and initiating affiliative approaches involve the occurrence of instantaneous events, for example making or receiving threatening gestures or vocalisations; moving as a response to such behaviour; making or receiving greetings. These behavioural categories complement the categories of grooming/being groomed and socially exploring which deal with social behaviour which is more prolonged.

Exploring for food: This behavioural category consists of all behaviour involved in actively searching for food (for example, turning over stones, or digging up grass sedges). It may also include locomotion when the subject is still within a food patch (e.g. a patch of *Cynodon* spp. grasses, or a flowering *Acacia* tree), and external processing of a selected food item before it is ingested (for example, pulling off the outer sheath of *Mariscus* sedge bases once they have been excavated). Figure 6.2



Figure 6.2: 'Exploring for food': all behaviour involved in actively searching for food.

illustrates this behavioural category. 'Exploring for food' is in part equivalent to Nicolson's (1982) 'foraging' (feed-walking = locomoting for more than three steps given that the subject has ingested food in the last minute), and may be included in other workers' definitions of the behavioural category 'feeding' (Pereira, 1984; Nicolson, 1982). This study separated 'exploring for food' from the behaviour of ingesting food to elucidate the acquisition of this skill.

Feeding: This behavioural category is defined so as to include only the ingestion of food, and being the category of highest priority, it is recorded even when another behaviour is occurring simultaneously. The start of a feeding bout is recorded as food items entered the mouth, and the end is recorded when chewing had stopped or when the subject had moved away from the food source. Nicolson (1982) defines 'feeding' to include ingestion of food items and their preparation, and Pereira (1984) defines the start of a feeding bout to be when a subject puts its mouth or hands in contact with a food item in any non-locomotory fashion. Comparisons of the data from this study with those from other studies can be made, but their inclusive nature has to be noted. 'Feeding' and 'exploring for food' behavioural categories were separated in this study to provide a more comprehensive account of the behaviour of young baboons, and to enable the calculation of rates of food ingestion, excluding food preparation time.

Statistical testing:

The methodology used in this study, where data were recorded continuously, enables the examination of behaviour with respect to the percentage of time spent in each activity, rather than with respect to frequency of occurrence and number of bouts.

In order to examine statistically whether there was age-related change in the amount of time spent in the various behavioural activities, data from young infants, older infants, juveniles and mothers were compared. Individuals from each age group were selected so as to provide the largest number of subjects of overlapping ages for which data were collected. This technique produced sample sizes of 3, 6, and 4 for young and older infants and juveniles respectively. A mean data value for the

percentage of time spent by each of these individuals in an activity was calculated from data over three consecutive months, to reduce the variance due to small sample sizes without introducing more variance by pooling data from a wide age range. The subjects selected are highlighted in Table 6.1. (Table 6.1 also notes the number of subjects for which data were collected at each age i.e. the number of subjects contributing to the mean values that are presented in the following figures.) These data were also compared with those of the 6 adult female subjects studied.

With the small sample sizes involved, it would be impossible to demonstrate normal distribution in these data. In the same way as Lee (1981) and Pereira (1984), I chose therefore to use non-parametric statistical tests when examining the data. The Kruskal-Wallis one way analysis of variance was used to examine whether the data from these four age groups were from the same population or whether there were differences between them. If the Kruskal-Wallis test indicated an overall significant difference in the data of the age groups (or the difference was close to significance), post-hoc Mann-Whitney tests were carried out in order to test between which groups the values were significantly different.

The additional notes on methodology in Chapter 5 which elaborate on a few aspects of this study also refer to the data presented in this chapter.

DEVELOPMENTAL CHANGE IN BEHAVIOURAL ACTIVITIES

In this section, data for each behavioural activity are presented and discussed separately, before a cumulative activity budget is generated in the next section. Figures 6.3 - 6.11 present the individual and mean data for infants and young juveniles 3 - 45 months old, by age (in months), for each of the behavioural activities described above. Mean values for the behaviour of adult females (i.e. mothers, selected as described in chapter 2) are also presented in these figures to provide an adult comparison for the activity budget data of the young subjects.

Table 6.1: The number of subjects and the months for which data were collected for each age, indicating subjects selected for statistical analysis: the individuals studied are denoted by their ID codes; IDs in parentheses indicate that data were recorded for contact/proximity categories only; square brackets, [], denote two individuals who were orphaned at the start of the study and thus were not included in the analysis of behaviour associated with the mother-infant relationship. N in parentheses indicates the number of subjects used in the analysis of m-i relations.

AGE	N	APR	MAY/JUN	JUL	AUG	SEP	OCT
3	2 (2)			DH MQ			
4	3 (4) (MC)		KK		DH MQ		
5	3 (3)			KK		DH MQ	
6	4 (4)		MC		KK		DH MQ
7	2 (4) (KO) (TP)			MC		KK	
8	2 (2)				MC		KK
9	3 (3)		KO TP			MC	
10	3 (4) (MO)			KO TP			MC
11	2 (4) (TY) (WG)				KO TP		
12	3 (5) (TT) (NP)		MO			KO TP	
13	5 (6) (EI)		TY WG	MO			KO TP
14	6 (6)		TT NP CP	TY WG	MO		
15	7 (6)		EI [BN]	TT CP	TY WG	MO	
16	7 (6)			EI [BN]	TT CP	TY WG	MO
17	6 (5)				EI [BN]	TT CP	TY WG
18	4 (3)					EI [BN]	TT CP
19	2 (1)						EI [BN]
28	0 (1) (TZ)						
29	- -						
30	1 (1)		TZ				
31	1 (1)			TZ			
32	1 (1)				TZ		
33	1 (1)					TZ	
34	1 (1)						TZ
35	0 (1) (EN)						
36	0 (1) (TC)						
37	1 (2) (NR)		EN				
38	2 (2)		TC	EN			
39	3 (3)		NR	TC	EN		
40	3 (3)			NR	TC	EN	
41	4 (3)		[BE]		NR	TC	EN
42	3 (2)			[BE]		NR	TC
43	2 (1)				[BE]		NR
44	1 (0)					[BE]	
45	1 (0)						[BE]

Moving:

Figure 6.3 presents the individual and mean data by age for the percentage of time spent moving. During the first year and a half of life, the mean percentage of time subjects spent independently moving increased with age, the most rapid increase being up to about 20% of time by the age of 6 months, after which the increase was slower, the values reaching about 30% by 18 months. For young juveniles, monthly means were mostly within the 20 - 40% range. (Apparent fluctuations in these mean values are probably caused by smaller sample sizes than for the infants.) The mean value for percentage of time spent moving independently by adult females was 30.5% (SE = 2.5).

Differences in the amount of time spent moving by groups of young infants, older infants, juveniles and mothers approached statistical significance (Kruskal-Wallis (K-W) test: $\chi^2 = 7.46$, $p = 0.059$). Young infants in fact spent significantly less time moving ($\bar{x} = 11.5\%$, SE = 3.0) than older infants ($\bar{x} = 29.6\%$, SE = 1.3), juveniles ($\bar{x} = 29.4\%$, SE = 0.8), and mothers (Mann-Whitney (M-W) U tests: $p = 0.020$, 0.034 and 0.020 respectively). The amount of time spent moving by older infants, young juveniles and mothers were not significantly different from each other.

Nicolson (1982) reports that the percentage of time spent moving appeared to increase steadily over the first year and then levelled off at the beginning of the second year at 21 - 24% of the time. She found that adult females spent 28% of their time moving, which is similar to the value in this study. For older subjects, Pereira (1984) found that young juveniles (1 - 2.3 years old) spent 24.7% of time moving, and that older juveniles (3 - 5.5 years) spent a very similar figure of 24.2% of time moving, again very similar values to those found in this study, though it is worth noting that figures for percentage of time spent in a behavioural activity for his groups of young and older juveniles (Pereira 1984, 1988) involve mean values from individuals varying greatly in age.

The data presented here therefore indicate a pattern of developmental change which is similar to that found in other studies, and where the time spent moving by

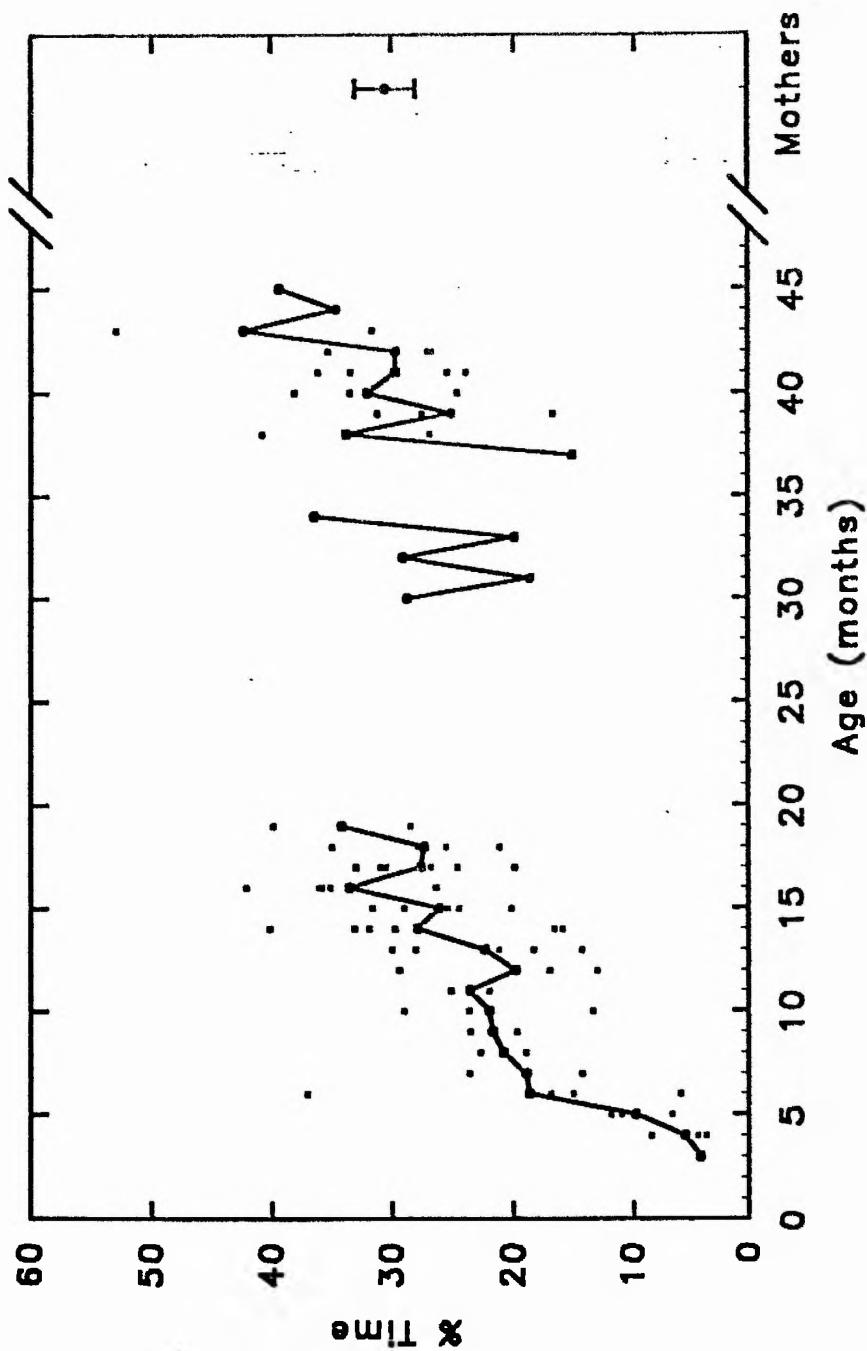


Figure 6.3: Percentage of time spent moving: small solid squares represent individual data for infants and young juveniles (3 - 45 months old); open squares joined by the line represent the means of these data by age (in months). The mean value for a group of mothers is presented, with standard error bar.

older infants (15 - 17 months old) was not significantly different from that spent by adult females.

Environmentally and socially exploring:

Figure 6.4(a) presents the mean and individual data for percentage of time spent environmentally exploring. The mean value was highest for infants of 3 months old, and then rapidly decreased with age in the following 5 months. A mean value of virtually 0% was reached around 15 months of age, indicating that individuals virtually ceased spending time environmentally exploring early in their second year. The adult female value for this activity was 0%. The amount of time spent environmentally exploring varied significantly across groups of young infants, older infants, young juveniles and mothers (K-W test: $\chi^2 = 16.30$, $p = 0.001$). Younger infants spent significantly more time environmentally exploring ($\bar{x} = 9.6\%$, $SE = 3.4$) than older infants ($\bar{x} = 0.5\%$, $SE = 0.1$) who spent more time in this behavioural activity than younger juveniles ($\bar{x} = 0.1\%$, $SE = 0.05$) (M-W U tests: $p = 0.020$ and 0.019 respectively). The group of mothers spent significantly less time environmentally exploring than young juveniles (M-W U test: $p = 0.018$).

Figure 6.4(b) presents the individual and mean data for the percentage of time spent socially exploring. Overall, the percentage of time spent in this behavioural category was much lower than that spent environmentally exploring: the highest individual value for percentage of time spent socially exploring was about 13%. Mean values varied to a greater extent than those for environmental exploring (though this may in part be due to the smaller magnitude of the values). The highest mean value for time spent in this behavioural category occurred at 5 months old. (N.B. the data at 37 months old is from only one individual, EN). The amount of time spent socially exploring generally declined as age increased. However, in contrast with 'environmental exploring', young juveniles still spent some of their time (around 1%) in this activity. The mean value for time spent socially exploring for the group of mothers is 0%. The percentage of time spent socially exploring varied significantly

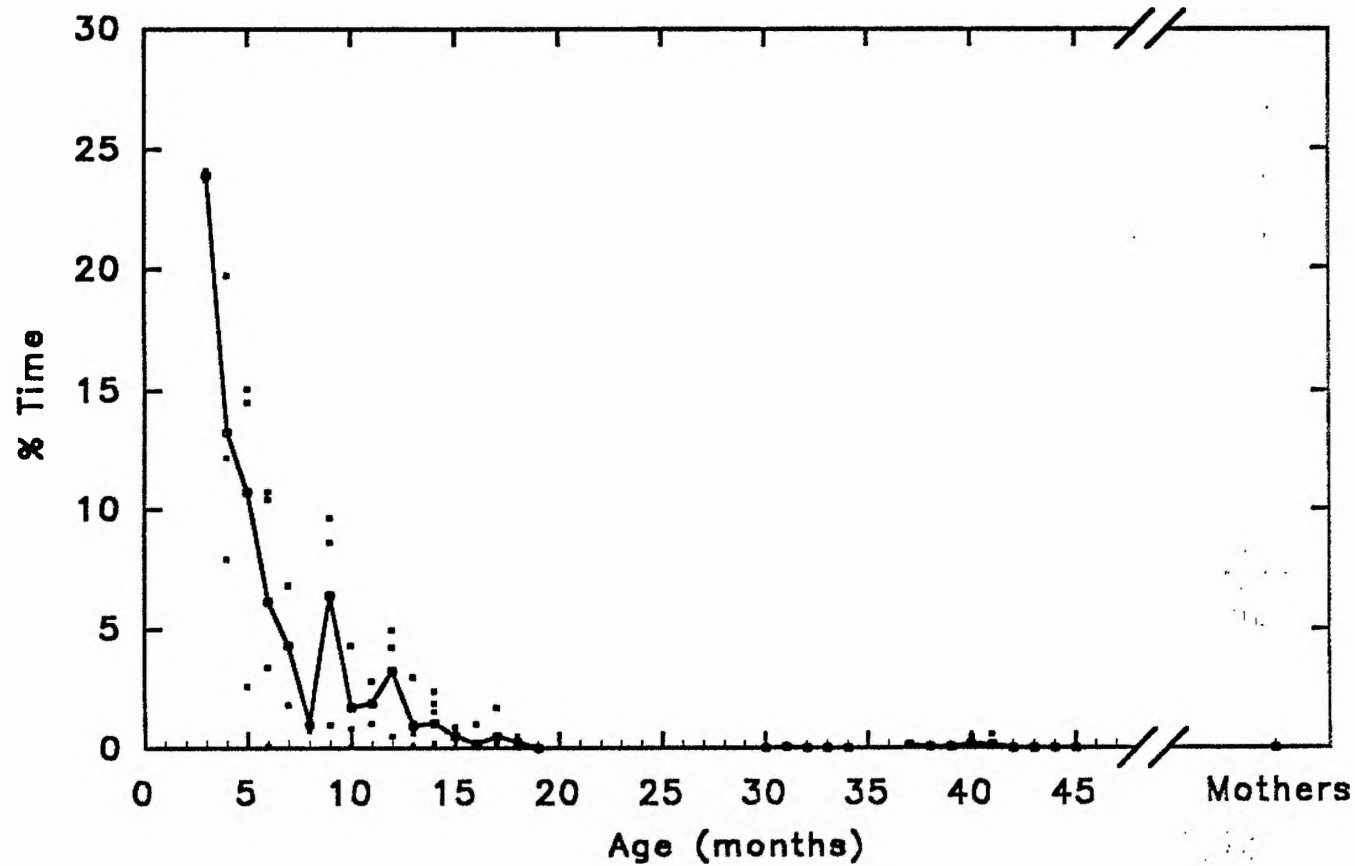


Figure 6.4(a): Percentage of time spent environmentally exploring:

small solid squares represent individual data for infants and young juveniles (3 - 45 months old); open squares joined by the line represent the means of these data by age (in months). The mean value for a group of mothers is presented, with standard error bar.

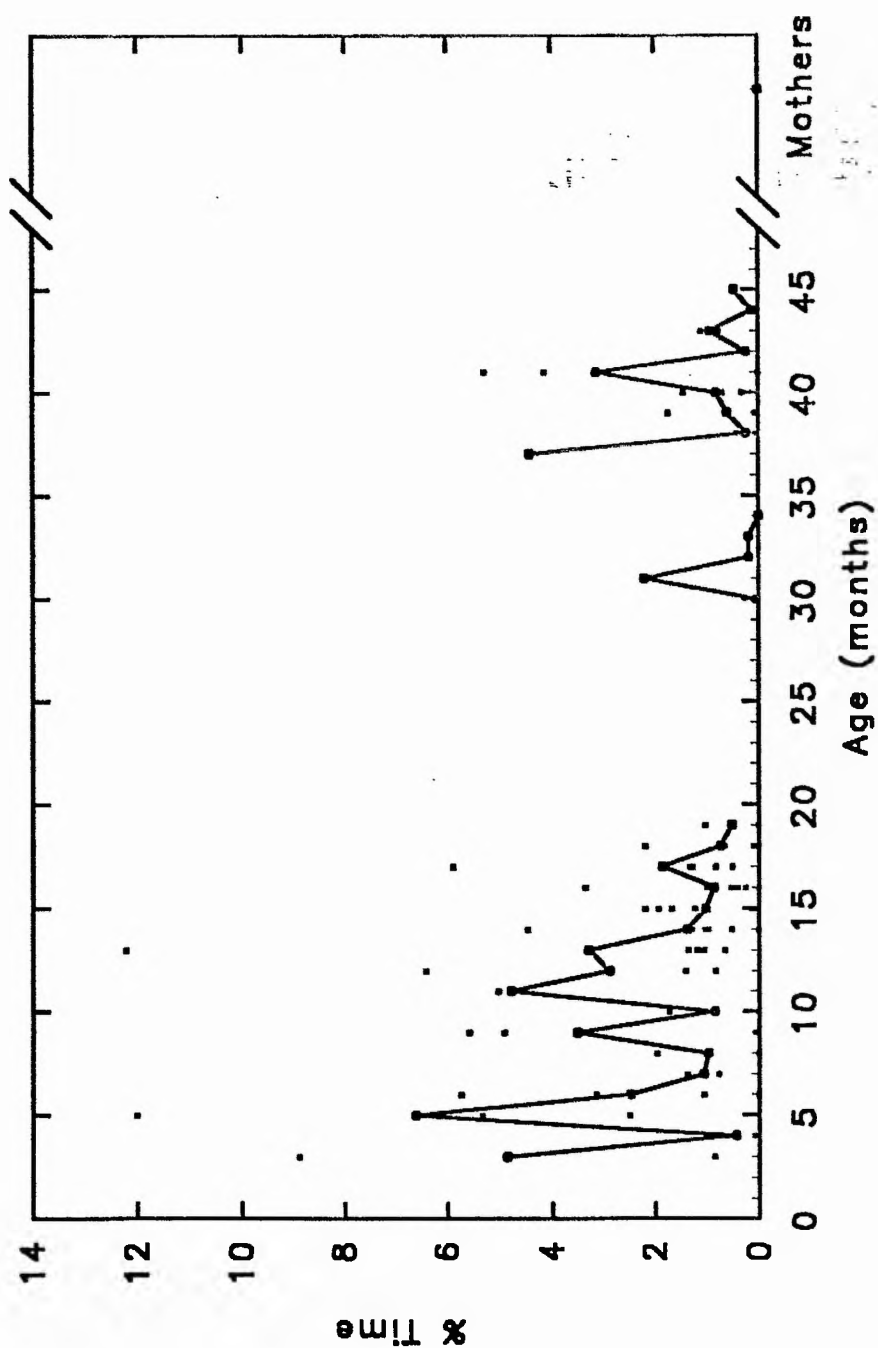


Figure 6.4(b): Percentage of time spent socially exploring: small solid squares represent individual data for infants and young juveniles (3 - 45 months old); open squares joined by the line represent the means of these data by age (in months). The mean value for a group of mothers is presented, with standard error bar.

across groups of young infants, older infants, young juveniles and mothers (K-W test: $\chi^2 = 14.4$, $p = 0.002$). The amount of time young infants spent socially exploring ($\bar{x} = 3.3\%$, $SE = 0.4$) was significantly more than that spent by juveniles ($\bar{x} = 1.5\%$, $SE = 0.4$) and by the group of mothers (M-W U tests: $p = 0.034$ and 0.011 respectively). Each group spent significantly more time socially exploring than the group of mothers (M-W U tests: $p = 0.003$ for older infants and 0.006 for juveniles), though there was no significant difference between the young infants and older infants, and older infants and young juveniles.

Exploratory interaction with the environment requires at least a certain level of mobility: at a very young age then, infants are not capable of this, and so initial values for percentage of time spent exploring would be zero. During the first month of life there must then be a rapid increase in the percentage of time spent exploring as physical development facilitates motion, possibly with percentage of time exploring accounting for a greater amount of the time in the second month of life than the values found here for the third month.

Although the category of 'social exploring' is similar to that of 'social play', studies of young baboons which have focused on or included the activity of social play report data which in some cases are not very similar to the results found in this study for 'social exploring'. Nash (1978) reports that the amount of play increased in frequency up to about 6 - 7 months of age before decreasing in months 8 - 10. This pattern of behaviour with a peak in amount of time spent playing in the middle of the first year was not found in the data from this study. Owens (1975) looked at the behaviour of males and females separately and found that males showed peaks in their amount of social play at 4.5 and about 14 months old, the amount of play decreasing thereafter. With a smaller sample of females he found greater fluctuation in the data where peaks were unidentifiable, but between 1 and 3 years of age, play remained at a fairly uniform level. He found consistent sex differences in the amount of play, where males played more than females. Robust sex differences in play have been reported by other workers: Pereira (1984) and Pereira and Altmann (1985) found sex differences in

the number and type of partners in play, and Nash (1978) reports that after 10 months of age the amount of play tended to decrease for females and increase for males. The distribution of male and female subjects in this study at different ages makes comparing their behaviour difficult. However, the combination of data from males and females in this study might explain the large amount of variation in the data presented here. The high variation in the data on 'social exploring' (Figure 6.4(b)) could also be a result of the mixed nature of this behavioural category.

Data from Pereira (1984), however, indicate that his young and older juveniles (see earlier) spent 1.6% and 1.1% time playing respectively. These figures are very similar to the values for older infants (>12 months old) and young juveniles in this study, and emphasise the fact that play/social exploring is not just a behaviour exhibited by young infants.

Data on the two types of exploring, 'environmental exploring' and 'social exploring', exhibit different age-related patterns. They both show a decline in the amount of time spent in that behaviour with increasing age, but whereas the age at which time is spent environmentally exploring is perhaps finite, some time is still spent in 'social exploring' behaviour even by young juvenile subjects. This suggests that the two types of exploring are functionally different. Martin and Caro (1985) suggest that different aspects of play may have separate motivations, different courses and different evolutionary origins. It is likely that this is true for these categories of exploring. Through environmental exploring, young baboons learn about their physical environment (clambering, playing alone and with natural objects etc.) and about potential food items: after a certain length of time, all that needs to be learnt has been done. The data for these subjects, where environmental exploring more or less ceased after 15 months, can be interpreted as being that period of time. There may be occasional periods (such as during a complete shift in the home range area to a place with a very different physical environment) when there will be some environmental exploration; however, these are exceptional cases. By contrast, the behavioural activities involved in 'social exploring' are part of a longer process of learning: as

individuals become older, their social relationships change and they may have to continue to spend time learning about their social environment.

Attending environmental and social:

The data presented in Figure 6.5(a) and (b) show that the percentage of time spent in these activities was low: for the majority of individuals, values were $<2\%$. For this reason, some care should be taken in interpreting these data.

Both behaviours exhibit a hint of a decrease in the percentage of time spent in that activity with increasing age though for 'attending environment', the highest mean value occurred at 4 months old. For the group of mothers, the mean values for percentage of time spent in these activities is very low but is greater than zero (attending environmental: $\bar{x} = 0.07\%$, $SE = 0.02$; attending social: $\bar{x} = 0.06\%$, $SE = 0.03$). The amount of time spent 'attending environmental' varied significantly between groups of young infants, older infants, young juveniles and mothers (K-W test: $\chi^2 = 12.35$, $p = 0.006$). In fact young infants, older infants and juveniles all spent significantly more time 'attending environmental' than the group of mothers (M-W U tests: $p = 0.02$, 0.01 and 0.011 respectively) but there were no significant differences between these groups. The amount of time spent 'attending social' also varied significantly between groups of young infants, older infants, young juveniles and mothers (K-W test: $\chi^2 = 10.16$, $p = 0.017$). The groups of young infants and older infants spent significantly more time 'attending social' than the group of mothers (M-W U tests: $p = 0.02$ and 0.01 respectively), but the group of juveniles only approached significance when their time spent 'attending social' was compared to that for mothers (M-W U test: $p = 0.055$). There were no significant differences between the behaviour of younger infants, older infants and juveniles.

These 'attending' categories of behaviour can be viewed as being precursors of environmental and social exploring, the active counterparts of these behaviours. As with visually attending (see below), the greater time spent in these behavioural activities by young baboons compared with their mothers suggests that these specific forms of

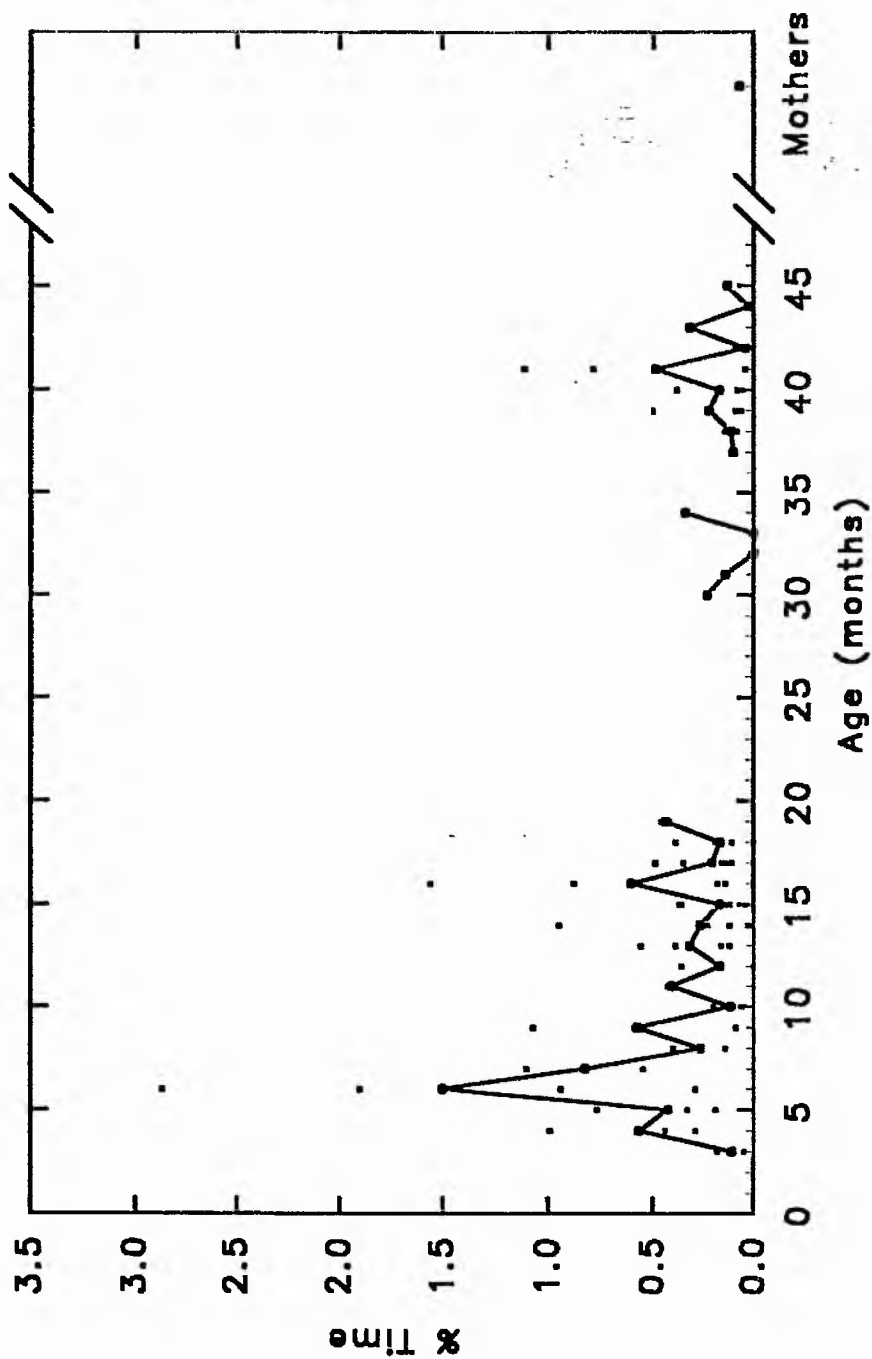


Figure 6.5(a): Percentage of time spent environmentally attending: small solid squares represent individual data for infants and young juveniles (3 - 45 months old); open squares joined by the line represent the means of these data by age (in months). The mean value for a group of mothers is presented, with standard error bar.

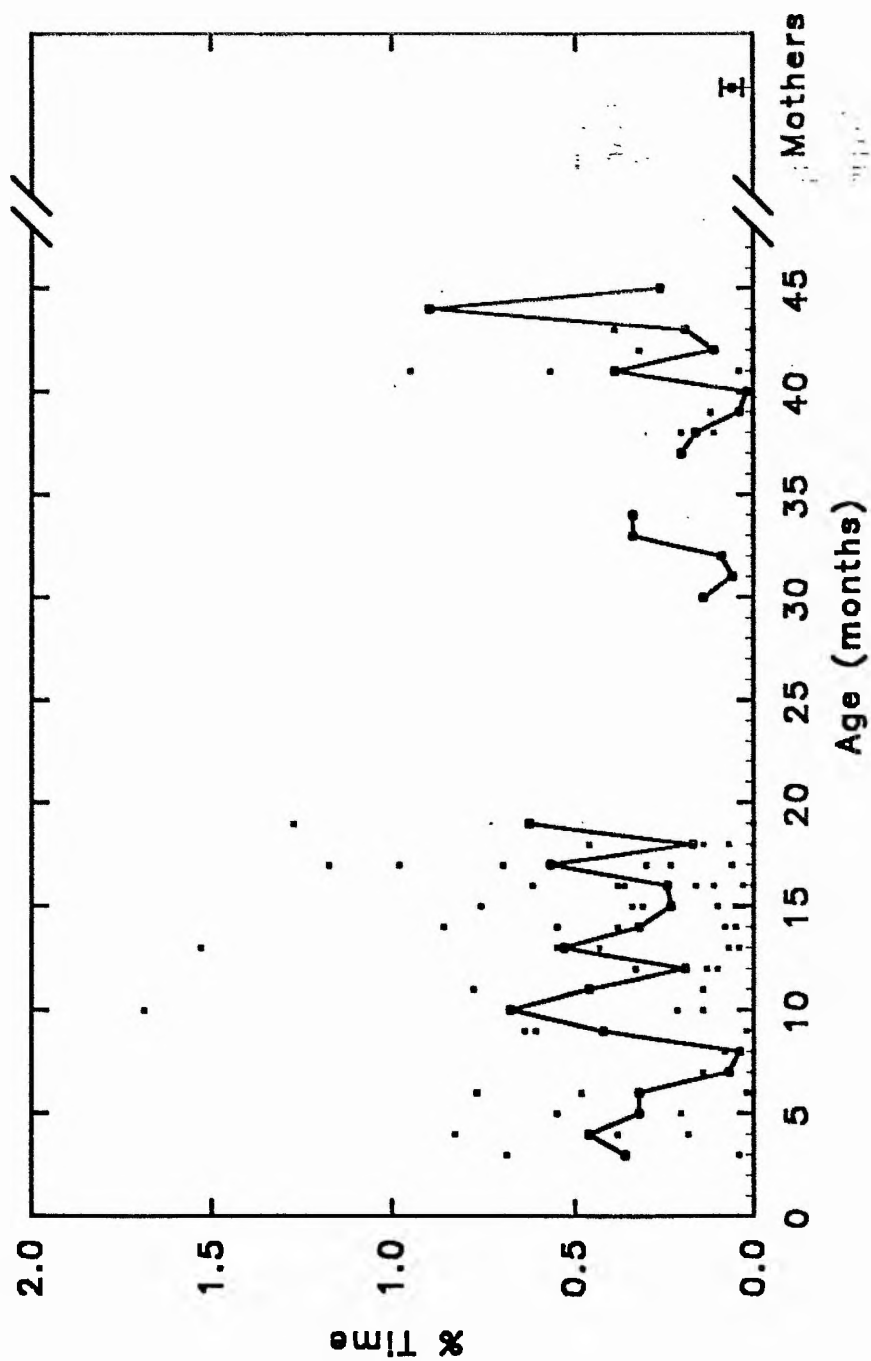


Figure 6.5(b): Percentage of time spent socially attending: small solid squares represent individual data for infants and young juveniles (3 - 45 months old); open squares joined by the line represent the means of these data by age (in months). The mean value for a group of mothers is presented, with standard error bar.

attending may be particularly important for young individuals providing them with information about social and environmental features.

Visually attending:

Figure 6.6 presents the individual and mean data for the percentage of time spent 'visually attending'. During infancy, there was a general decrease in the mean values as age increased, from around 23% to around 7%. Mean values for percentage of time spent visually attending by juveniles were similarly around 6 - 10% and the mean value for the group of mothers was 7.0%. The amount of time spent 'visually attending' varied significantly across the groups of young infants, older infants, young juveniles and mothers (K-W test: $\chi^2 = 10.49$, $p = 0.015$). The amount of time young infants spent in this behavioural activity ($x = 20.4\%$, $SE = 1.8$) was significantly more than the other groups (older infants: $x = 8.8\%$, $SE = 1.3$; juveniles: $x = 10.1\%$, $SE = 1.6$) (M-W U tests: with older infants, $p = 0.02$; juveniles, $p = 0.034$; mothers, $p = 0.02$), though the amount of time spent by other groups was not significantly different from each other.

With no data available on the behaviour of individuals of <3 months old, it is not feasible to say whether the high values for percentage of time spent visually attending are a peak or whether a peak occurred earlier. It is probable that for very young infants the percentage of time being spent visually attending as defined in this study would be zero, but with these data it is realistic only to say that an initial value for percentage of time spent visually attending is indeterminable.

Many records of subjects 'visually attending' were made while they were being carried dorsally by their mothers. This may therefore in part account for the high values of 'visually attending' in the first 7 months of life while infants are still being transported by their mothers. During this time, young infants are likely to be learning about their environment even though they are not interacting with it.

Because of the definition of 'visually attending' used in this study, data are more comparable with those of 'resting' in other studies, and so will be discussed below.

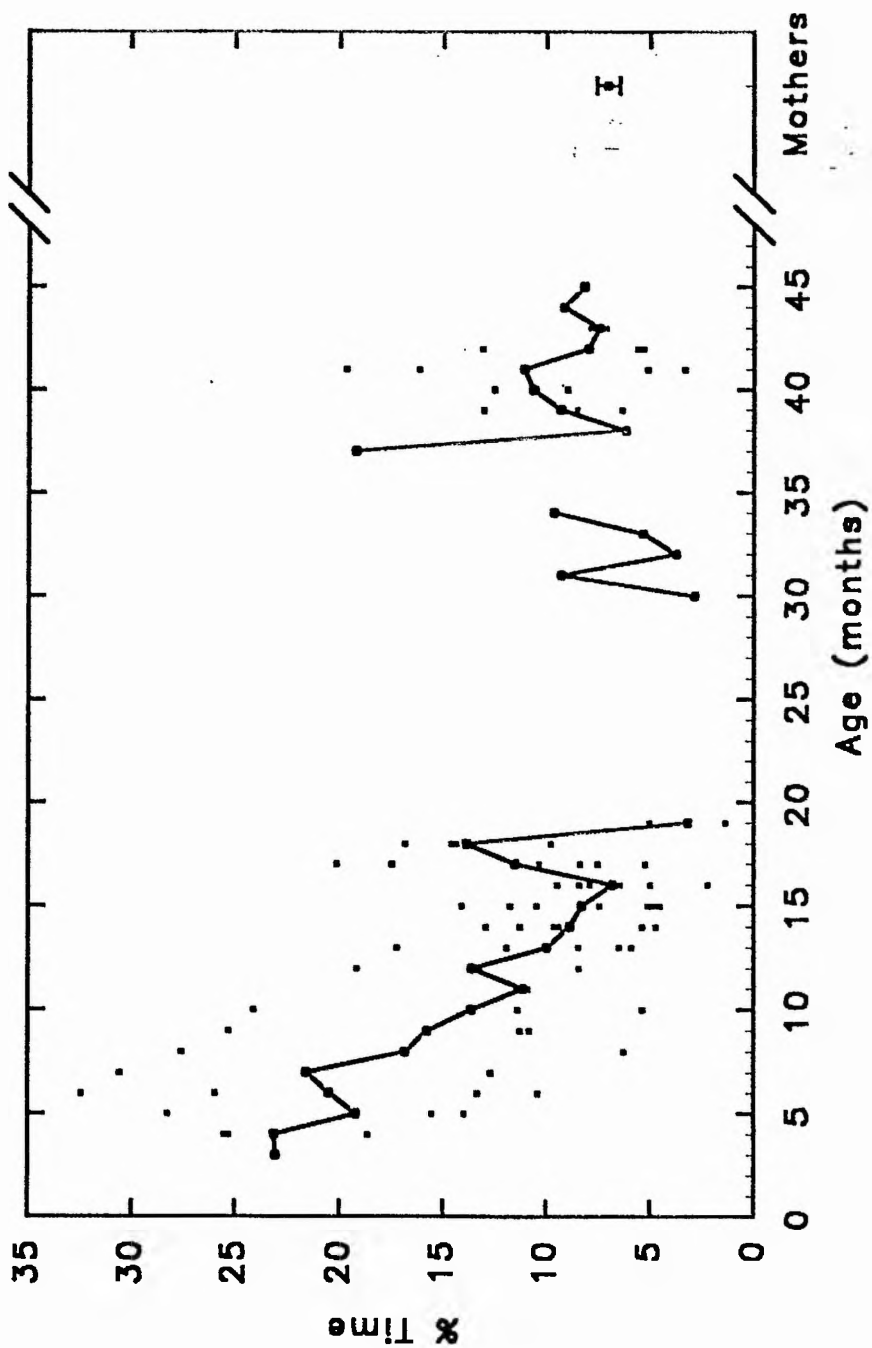


Figure 6.6: Percentage of time spent visually attending:

small solid squares represent individual data for infants and young juveniles (3 - 45 months old); open squares joined by the line represent the means of these data by age (in months). The mean value for a group of mothers is presented, with standard error bar.

Resting:

Figure 6.7 presents the individual and mean data for the percentage of time spent resting. It is important to note that the behavioural category of resting used in this study had the lowest recording priority of all behavioural categories (see Chapter 2). I feel this category was used appropriately in clear circumstances, but at other times there may have been a tendency to assign a more highly ranking behavioural category to the behaviour being observed rather than record the behaviour as being 'just' resting ('out-of-sight' was the only category of lower priority, but this was very specifically used). The following description and discussion of 'resting' should therefore be treated with some caution.

The data show a general decrease in mean value as age increased, so that by about 9 months of age, infants spent very little time resting. (N.B. the unusually high data point at 37 months old is from one individual, EN.) The mean value for the group of mothers was 0.4% (SE = 0.2). The percentage of time spent resting by groups of young infants, older infants, young juveniles and mothers varied significantly (K-W test: $\chi^2 = 8.18$, $p = 0.043$). The amount of time spent resting by young infants ($\bar{x} = 6.4\%$, SE = 2.1) was significantly more than for the other groups (older infants: $\bar{x} = 1.0\%$, SE = 0.6; juveniles: $\bar{x} = 0.3\%$, SE = 0.3) (M-W U tests: $p = 0.039$ with older infants; 0.032 with juveniles; 0.018 with mothers). Differences in the time spent resting between the other groups were not significant. The difference in percentage of time spent resting between an adult and a growing infant is as might be expected.

Pereira (1984) reports that his young and older juveniles spent 18.6% and 20.7% of time resting respectively. Clearly, and as I have already mentioned (see visually attending section), the values reported for the amount of time spent resting in other studies of behavioural activity budgets are much higher than those presented here. Combining the data from the behavioural categories resting and visually attending would produce data which are more similar in nature to the category of resting used by

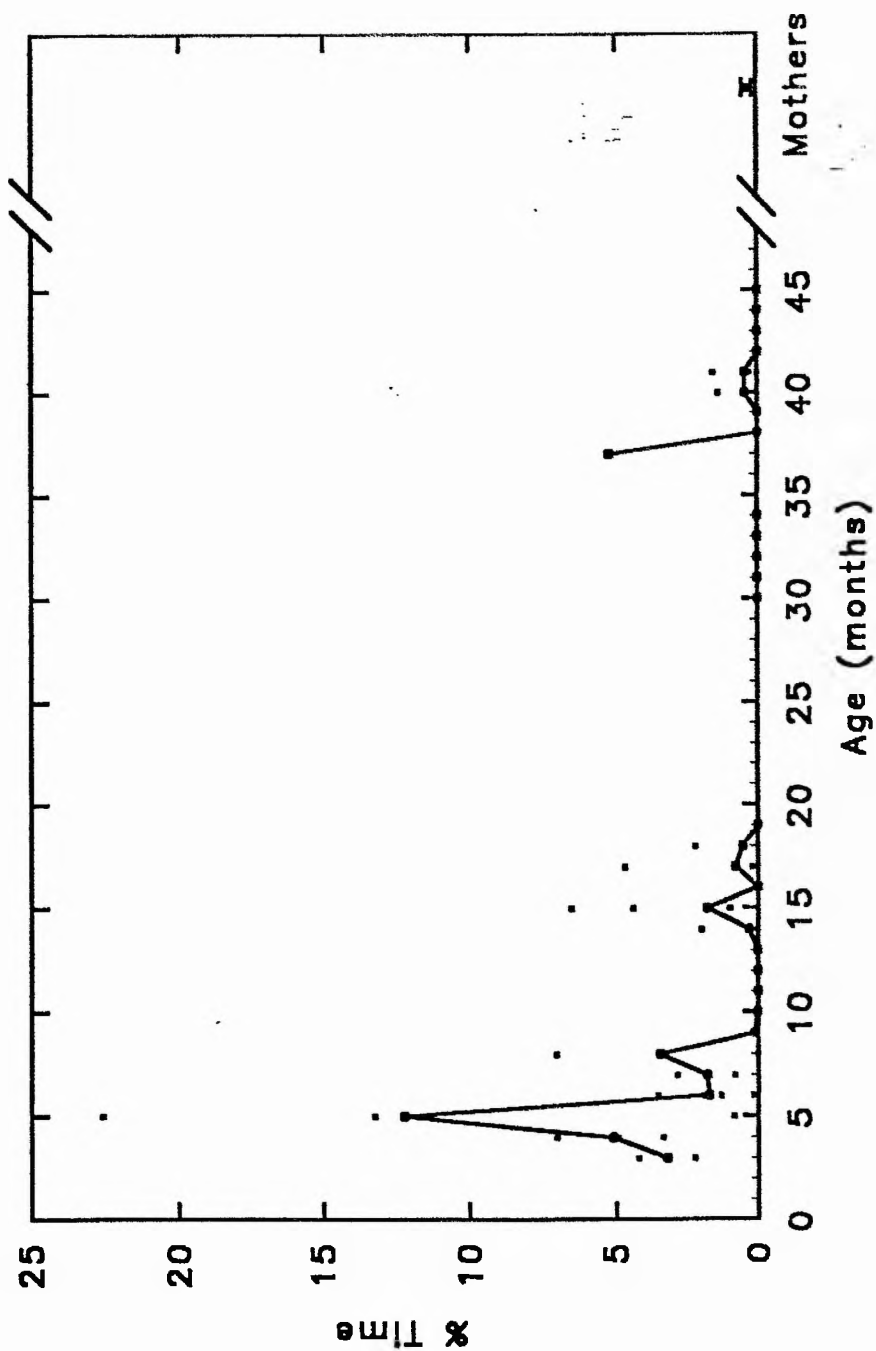


Figure 6.7: Percentage of time spent resting: small solid squares represent individual data for infants and young juveniles (3 - 45 months old); open squares joined by the line represent the means of these data by age (in months). The mean value for a group of mothers is presented, with standard error bar.

other workers. It would mean that values for percentage of time spent 'resting' for subjects in their second year of life and older are about 5 - 10%. If a certain amount of time in an individual's activity budget must be conserved for resting (Dunbar, in press), then differentiating resting with eyes shut or being asleep from 'resting' with eyes open, immobile but alert (= 'visually attending') as in this study, elucidates the fact that it is the latter kind of resting which older individuals (>10 months old) maintain as a behavioural activity rather than spending time during the day sleeping. Much 'resting' by young infants in the first 7 months is therefore done while riding on their mothers' backs i.e. 'visually attending'.

Being groomed and grooming:

Individual and mean data for the percentage of time spent being groomed and grooming are presented in Figure 6.8(a) and (b) respectively. Since the behavioural categories 'on the nipple' and 'in nipple position' were ranked as higher priority than grooming or being groomed during data collection in this study, if an infant was on or at its mother's nipple and it was simultaneously being groomed by (most likely) its mother, then the activity recorded was on or at the nipple; such grooming behaviour was ignored until for example the infant stopped suckling but continued to be groomed. Values for percentage of time being groomed presented here are therefore slight underestimates of the time spent in grooming as a whole.

Examining the data for being groomed (Figure 6.8(a)), there is no clear age-related change in the percentage of time spent in this activity, which contrasts with the behaviours discussed above. The amount of time spent being groomed by groups of young infants, older infants, juveniles and mothers did not vary significantly (K-W test: $\chi^2 = 2.78$, $p = 0.427$). However, these data suggest that over the first 6 months of data, there is a decrease in the percentage of time spent being groomed. The mean value dropped from 3.7% at 3 months of age to effectively zero at 6 - 8 months of age ($N = 2 - 4$), before rising again to remain at values of about 2% for later ages. This pattern of behaviour could be interpreted as part of the process of weaning

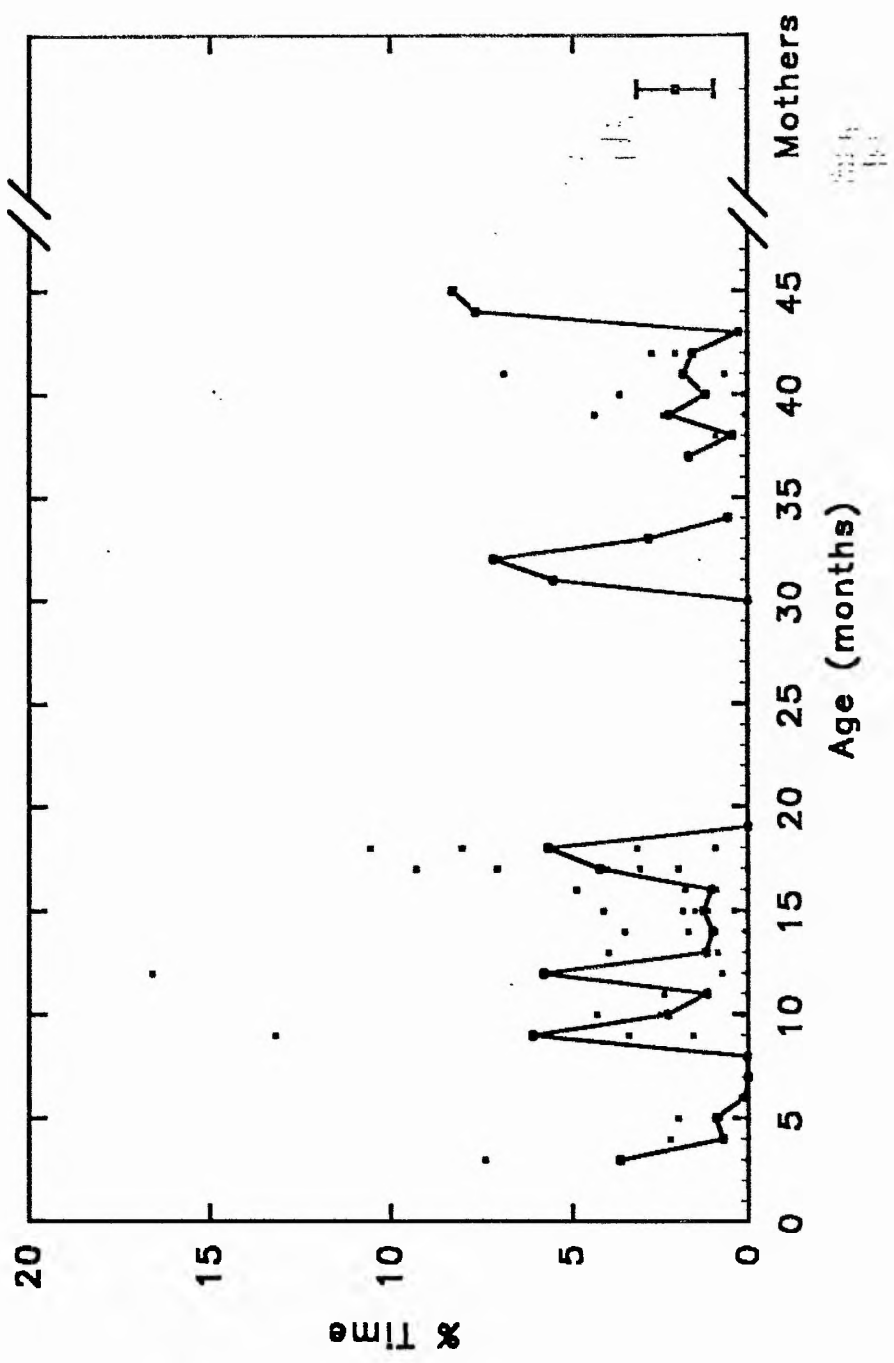


Figure 6.8(a): Percentage of time spent being groomed: small solid squares represent individual data for infants and young juveniles (3 - 45 months old); open squares joined by the line represent the means of these data by age (in months). The mean value for a group of mothers is presented, with standard error bar.

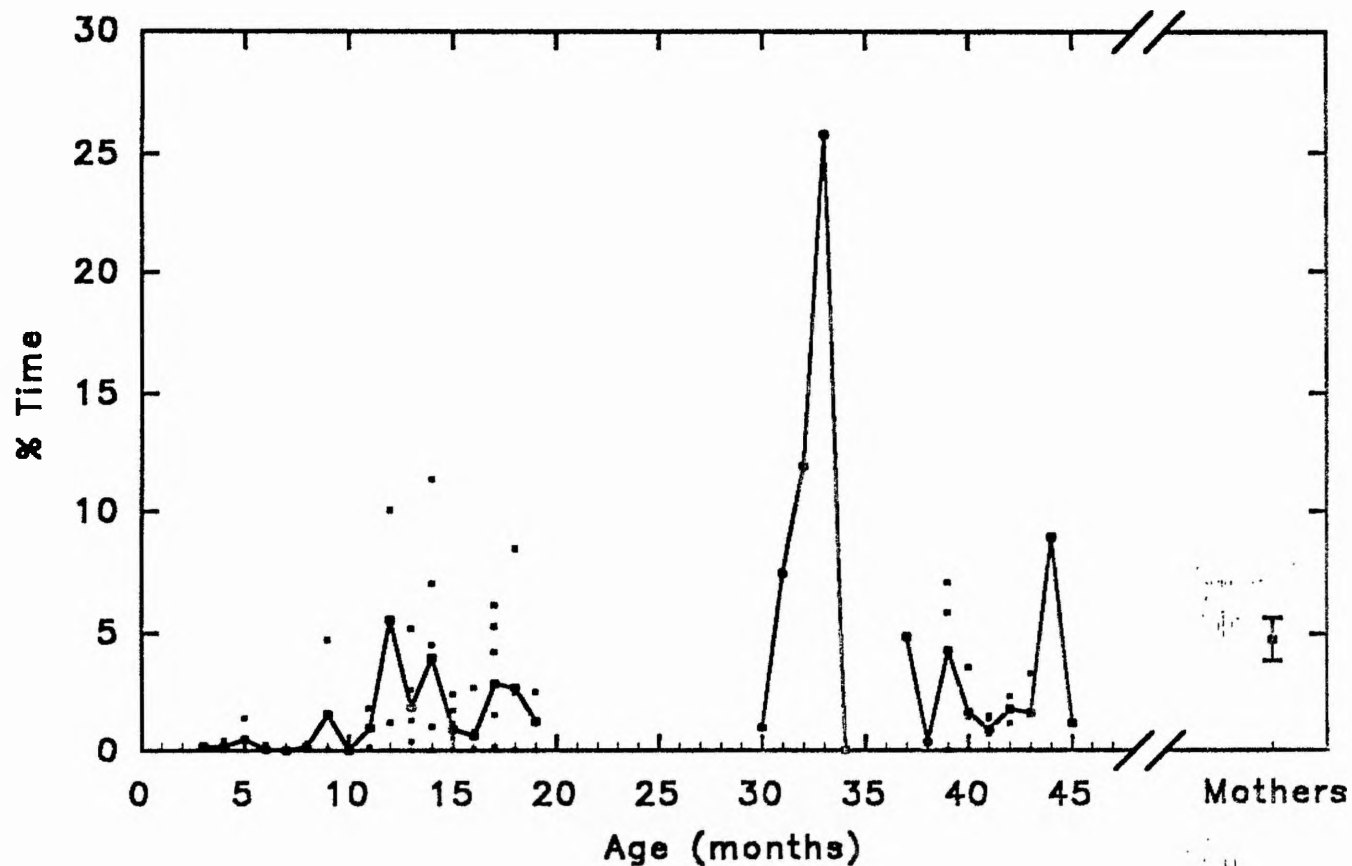


Figure 6.8(b): Percentage of time spent grooming:

small solid squares represent individual data for infants and young juveniles (3 - 45 months old); open squares joined by the line represent the means of these data by age (in months). The mean value for a group of mothers is presented, with standard error bar.

whereby, like time spent in contact and at the nipple (see Chapter 5), the amount of time infants spent being groomed by the mother decreases; then around 9 - 10 months old infants resume being groomed, but on a different basis, indicative of the changed relationship with their mothers. Examining the identity of the groomers would elucidate this interpretation.

Nash (1978) reports data which are similar to those found in this study (although 90% of her observations were made before 1300hr and therefore potentially unrepresentative of whole day activity budgets: Pereira (1984) has shown that the proportion of time spent in social activity is generally highest at the start of the day). Her data show that a high proportion of time was spent being groomed at 3 months old ($N = 1$ for this early age), but then the amount of time spent being groomed dropped between 6 and 8 months old, thereafter rising slightly and reaching a fairly constant level. These high values for the time spent being groomed at a young age are likely to be indicative of the large amount of time that young infants spend in contact with their mothers, but also the level of interest and attention which young infants receive from other members of the troop. Examining the identity of the groomer would elucidate the nature of these high values. The drop in percentage of time spent being groomed would then correspond with the periods when interest in the infant wanes, and when the infant starts spending more time away from its mother. The increase in the percentage of time spent being groomed at the end of the first year of life would correspond with the period when infants are moving increasingly on their own and exploring, probably picking up a larger amount of ectoparasites and dirt than when they were in contact with their mother, and also the time at which an infant is now starting to interact with a larger number of individuals in the troop. There is no evidence in these data of a peak in being groomed as a response by the mother during the rejection process.

Nash (1978) also found and documented considerable individual variation in her data (for all behavioural categories, she presents data for each individual). She draws attention to the important fact that clearly each infant has different behavioural characteristics and experiences in addition to those related to the sex of the individual,

something which I readily agree with.

The data for grooming (Figure 6.8(b)) indicate that aside from an exaggerated set of mean values from the one individual aged 30 - 34 months, values for the percentage of time spent grooming are generally less than 10%. Until 9 months of age, infants spent virtually 0% of their time grooming other individuals. The mean adult female value for time spent grooming is 4.8% (SE = 0.9). Differences in the amount of time spent grooming varied significantly between groups of young infants, older infants, juveniles and mothers (K-W test: $\chi^2 = 13.38$, $p = 0.004$). There was in fact no significant difference between the behaviour of young infants and older infants (M-W U test: $p = 0.121$), but young infants spent less time grooming than juveniles and the group of mothers (M-W U tests: $p = 0.034$ and 0.020 respectively). Each group of young baboons also spent significantly less time grooming than the group of mothers (M-W U tests: $p = 0.020$, 0.004 and 0.033 respectively).

Nash (1978) similarly found that infants rarely groomed other individuals in the early months of their lives. Pereira (1984) reports mean values of 5.8% and 8.4% time spent grooming by his young and older juveniles (1 - 2.3 and 3 - 5.5 years respectively), which are similar to those found in this study. Pereira and Altmann (1985) report that grooming relations are asymmetrical, where older group members are willing to groom younger ones, but younger members are more willing to be groomed. The amount of time spent grooming in this study shows an age-related change which is consistent with these previous studies: time spent grooming is virtually zero until the infant starts to become independent and then increases with increasing age, as the infant reciprocates grooming rather than just receiving grooming.

Again it would be particularly interesting to look at who is grooming and being groomed by these young baboons. At around the time of weaning, infants' partners in grooming are more often their mothers and this is less often the case with older juveniles (Pereira, 1984; Pereira and Altmann, 1985). Mothers are more likely to put up with unskilled grooming and are less likely to require reciprocation for the grooming they give their infants. Reciprocity in grooming increases with age (Pereira, 1984).

By looking at the identity of grooming partners, changes in the level of reciprocity, the age-sex group of the partners and the role mothers play in their infants' grooming activities could be elucidated. Chapter 5 revealed that juvenile baboons still maintained a degree of contact with their mother even in their fourth year and this is certainly likely to be associated with grooming. It is also likely that there is a sex difference in the amount of time older infants and young juveniles spend grooming with their mother because of their different behaviour as adolescents. Females remain in their natal troop and become part of strong matrilineal social structures, within which grooming in the form of a mother-infant-sibling relationship continues to operate long after infants have been weaned.

Receiving aggression, initiating aggression, and avoiding:

These behavioural categories are by definition of brief duration, so the values for percentage of time spent in these activities are low. Examining the mean values of percentage of time spent receiving and initiating aggression and avoiding, there is no evident change in behaviour with increased age, but since the values are generally $<0.3\%$, it is really inappropriate to discuss these behaviours in the context of activity budgets. It would be more appropriate to look at the frequency of occurrences of these behavioural categories.

It is worth noting though that individuals' data for percentage of time spent initiating aggression show there are no occurrences before the age of 8 months old. Initiating aggression is therefore something which is absent from the behavioural repertoire of very young infants and something that they acquire at an older age.

Receiving and initiating affiliative approaches:

As with the behavioural categories discussed above, making and receiving a greeting is an instantaneous occurrence of short duration. Because of this, the data for these behavioural activities were analysed with respect to the frequency of occurrence of these events at each age (in months) as well as the percentage of time spent in the

activity at each age. The individual and mean data for the frequency of initiating and receiving affiliative approaches per hour are presented in Figure 6.9(a) and (b); the individual and mean data for the percentage of time spent initiating and receiving affiliative approaches are presented in Figure 6.9(c) and (d). Both techniques resulted in similar patterns of data for these behavioural activities, and the mean data for percentage of time spent initiating and receiving affiliative approaches correlated strongly with those for the frequency of these events (initiating affiliative approaches: $R = 0.93$, $p < 0.001$; receiving affiliative approaches: $R = 0.95$, $p < 0.001$). Developmental change in the percentage of time spent in these activities can therefore still be discussed in order to be incorporated into later discussions of activity budgets.

There is no significant variation in the amount of time spent initiating affiliative approaches by young infants, older infants, juveniles and mothers. Figure 6.9(c) shows that there is a fair amount of variation in the mean values, but for all groups they are comparable with the mean value for adult females of 0.25%.

However, the data for receiving affiliative approaches (Figure 6.9(d)) show a clear decrease in the mean percentage of time spent in that activity with increasing age for infant subjects. Variation in the amount of time spent receiving affiliative approaches by groups of young infants, older infants, juveniles and mothers approached significance (K-W test: $\chi^2 = 7.28$, $p = 0.063$). In fact the amount of time young infants spent receiving affiliative approaches ($\bar{x} = 0.49\%$, $SE = 0.02$) was significantly greater than the values for older infants ($\bar{x} = 0.11\%$, $SE = 0.02$), juveniles ($\bar{x} = 0.90\%$, $SE = 0.02$) and mothers ($\bar{x} = 0.10\%$, $SE = 0.03$) (M-W U tests: $p = 0.02$, 0.034 and 0.02 respectively), though none of these latter groups were significantly different from the others. The initially relatively high values for percentage of time spent receiving greetings and affiliative approaches corresponds with the unusually high interest that members of the troop other than the mother (particularly adult and sub-adult females) show in recently born infants. The interest in any particular infant wanes as the infant becomes older and as other infants are born, and this would explain the decrease in the greetings and attention that infants receive as

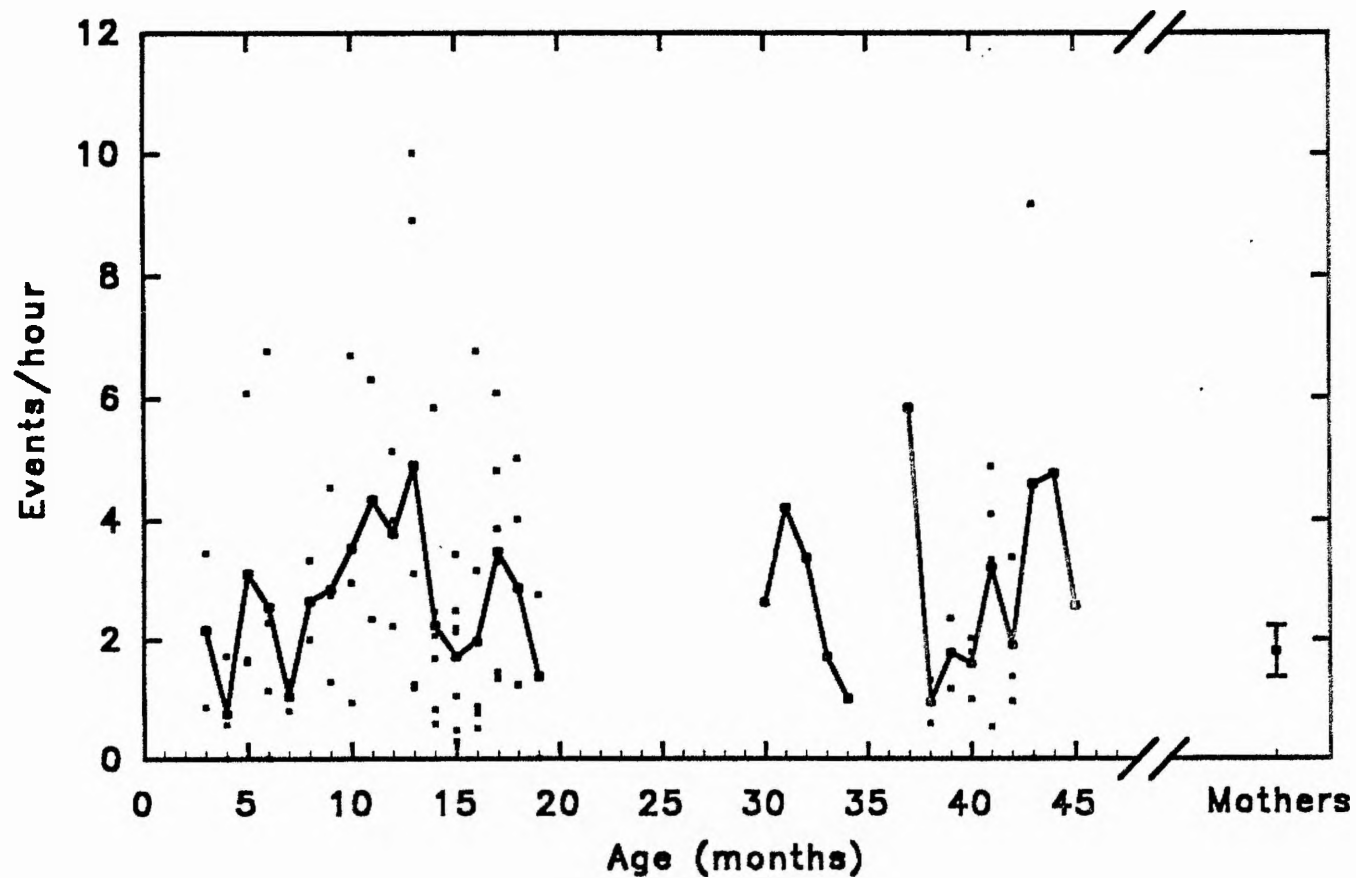


Figure 6.9(a): Frequency of initiating affiliative approaches /hour:

small solid squares represent individual data for infants and young juveniles (3 - 45 months old); open squares joined by the line represent the means of these data by age (in months). The mean value for a group of mothers is presented, with standard error bar.

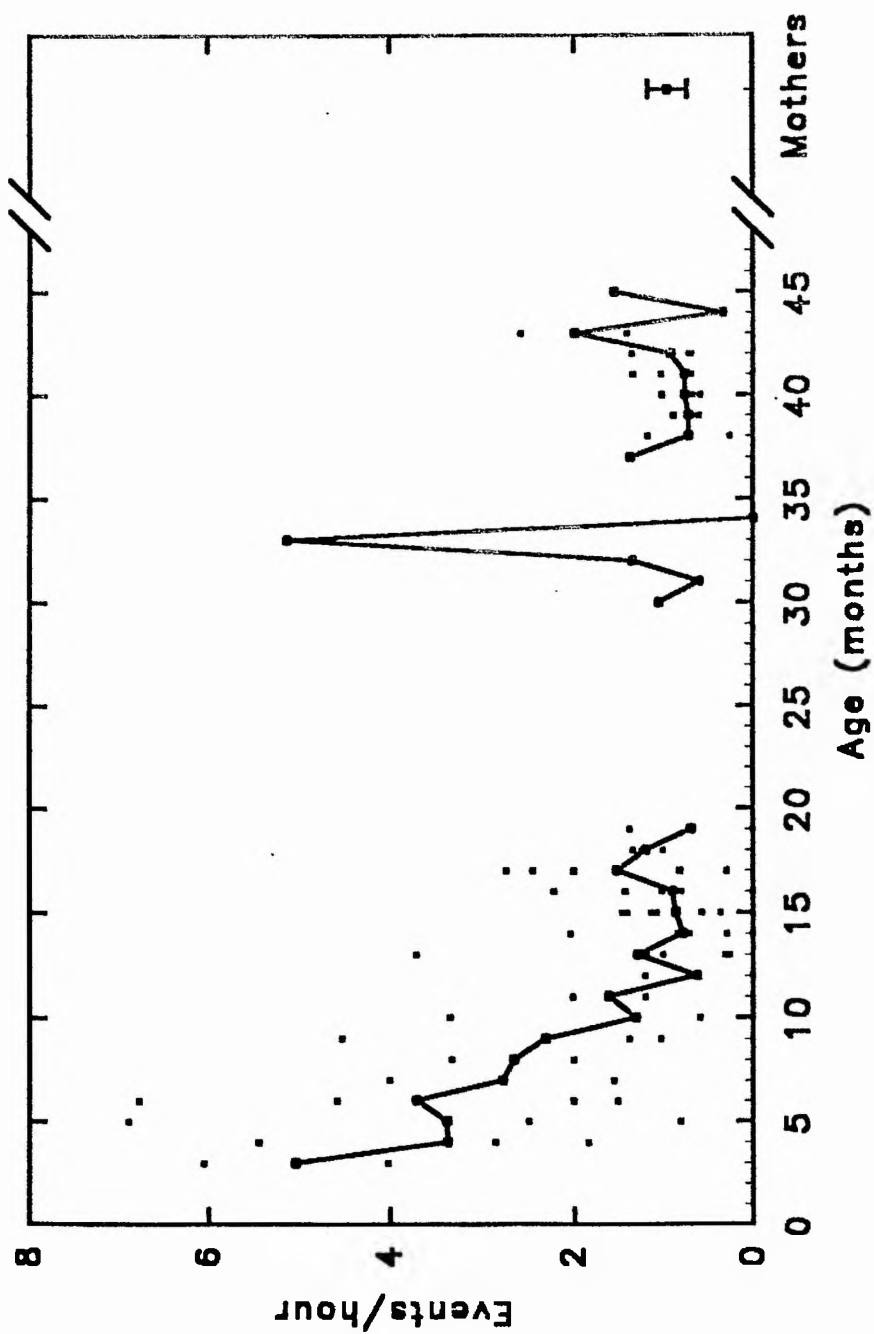


Figure 6.9(b): Frequency of receiving affiliative approaches /hour:

small solid squares represent individual data for infants and young juveniles (3 - 45 months old); open squares joined by the line represent the means of these data by age (in months). The mean value for a group of mothers is presented, with standard error bar.

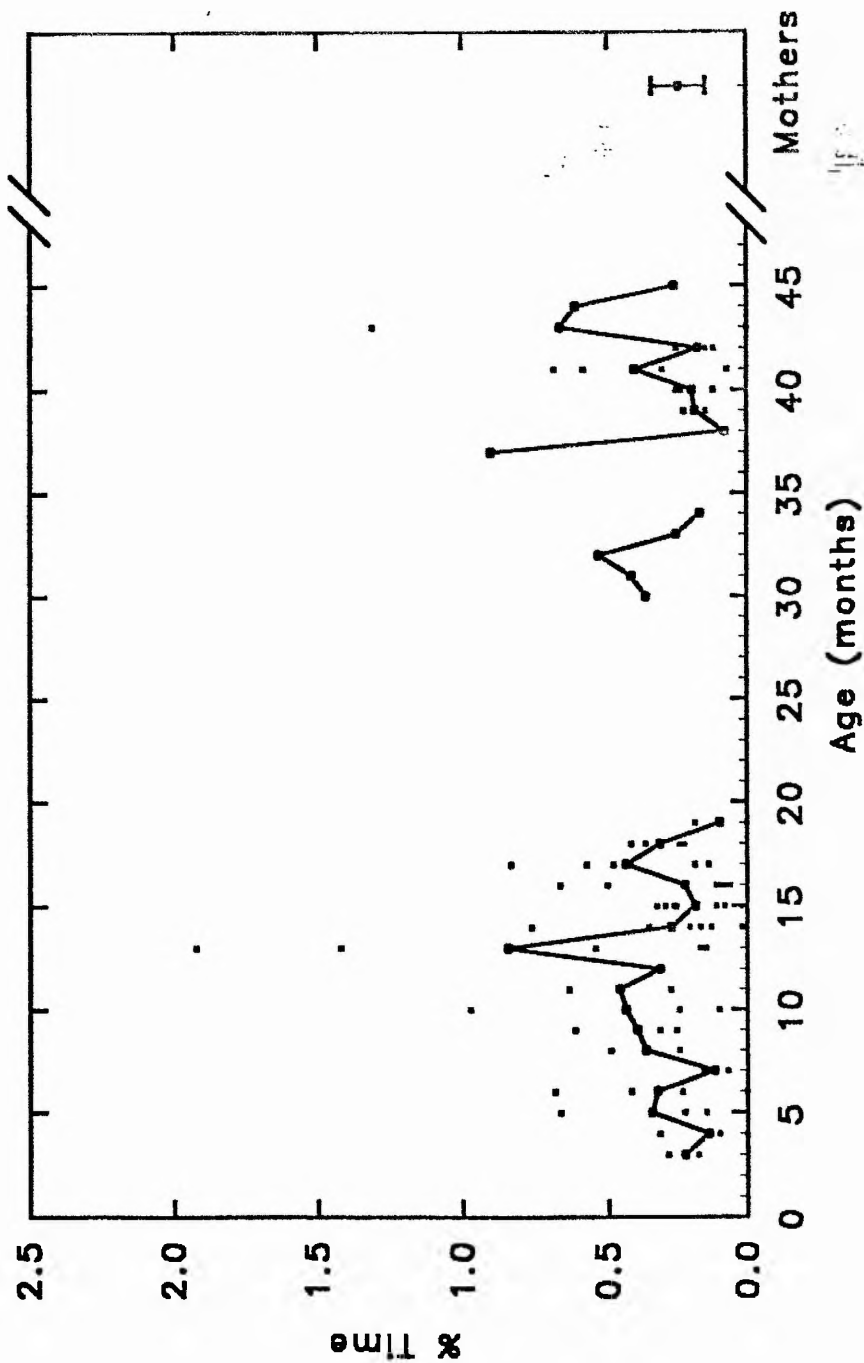


Figure 6.9(c): Percentage of time spent initiating affiliative approaches: small solid squares represent individual data for infants and young juveniles (3 - 45 months old); open squares joined by the line represent the means of these data by age (in months). The mean value for a group of mothers is presented, with standard error bar.

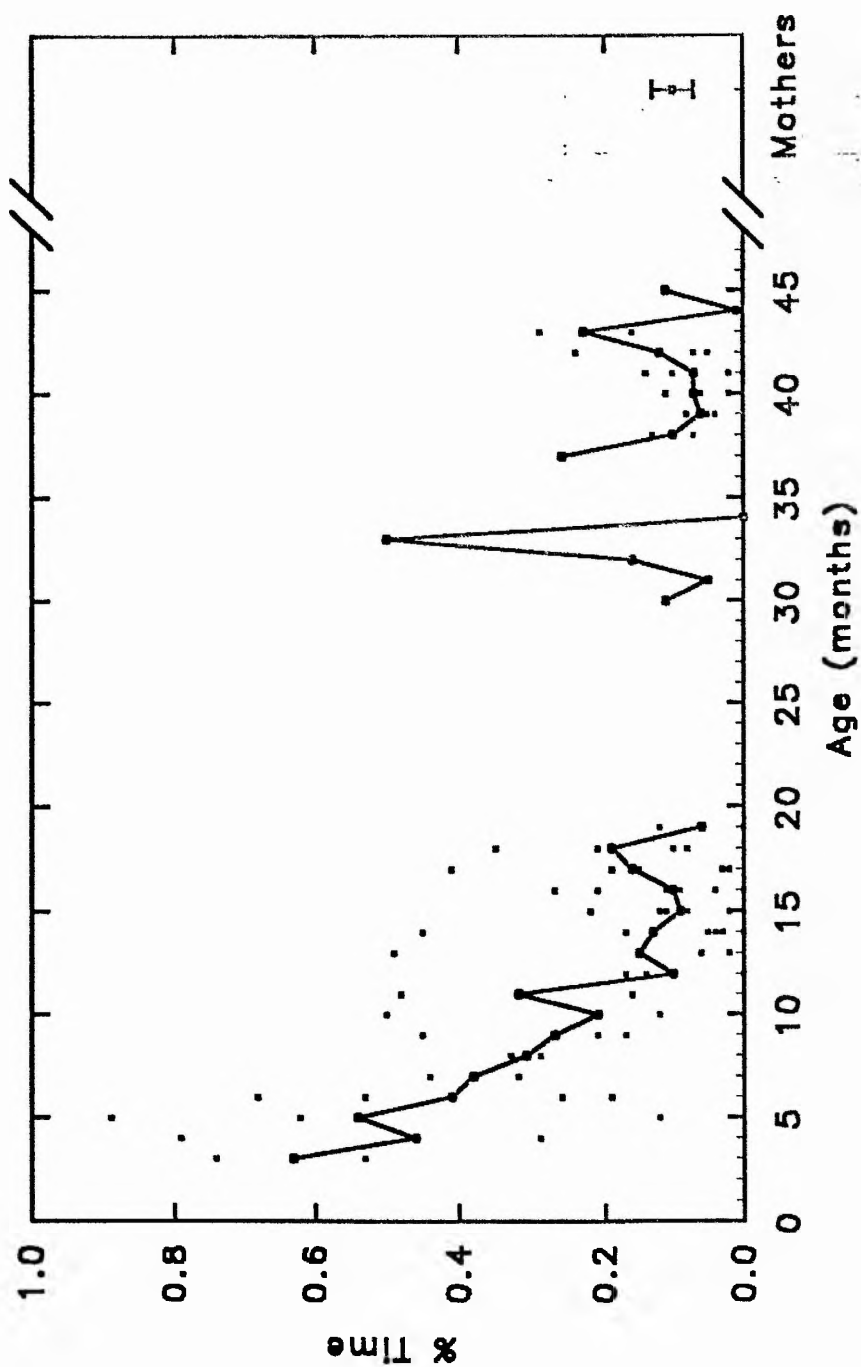


Figure 6.9(d): Percentage of time spent receiving affiliative approaches: small solid squares represent individual data for infants and young juveniles (3 - 45 months old); open squares joined by the line represent the means of these data by age (in months). The mean value for a group of mothers is presented, with standard error bar.

their age increases, so that by around one year old they are no longer receiving higher than average affiliative approaches.

Exploring for food:

The individual and mean data for the percentage of time spent exploring for food are presented in Figure 6.10.

The mean values for percentage of time spent in this activity show a rapid increase over the ages of 3 - 5 months old from a value of close to zero to values of around 10%, and then, the mean value for percentage of time spent exploring for food decreased slowly with the increasing age of the subjects. The mean value for a group of mothers is 3.8% (SE = 0.3). The overall difference between groups of young infants, older infants, juveniles and mothers in the amount of time spent exploring for food was significant (K-W test: $\chi^2 = 12.36$, $p = 0.006$). Young infants ($\bar{x} = 7.2\%$, SE = 1.0), older infants ($\bar{x} = 7.8\%$, SE = 0.6) and young juveniles ($\bar{x} = 6.8\%$, SE = 0.8) all spent more time exploring for food than did the group of mothers (M-W U tests: $p = 0.02$, 0.004 and 0.011 respectively), but there were no significant differences in the time spent exploring for food between these groups.

The ability to forage for edible food is one of the skills acquired during infancy as a necessary part of the process of becoming nutritionally self-sufficient. The data presented in Figure 6.10 can be interpreted as demonstrating a period in young infancy when a large amount of time is spent in this activity while the skill is first learnt. After a certain amount of learning, the action of exploring for food may actually become more efficient so that at an older age, less time is required to be spent in this activity, and the time that was necessary for the learning to take place is no longer needed. Adults therefore spent less time exploring for food.

Feeding:

Figure 6.11 presents the individual and mean data for percentage of time spent feeding on solid foods i.e. not feeding on milk or water. The data show a steep

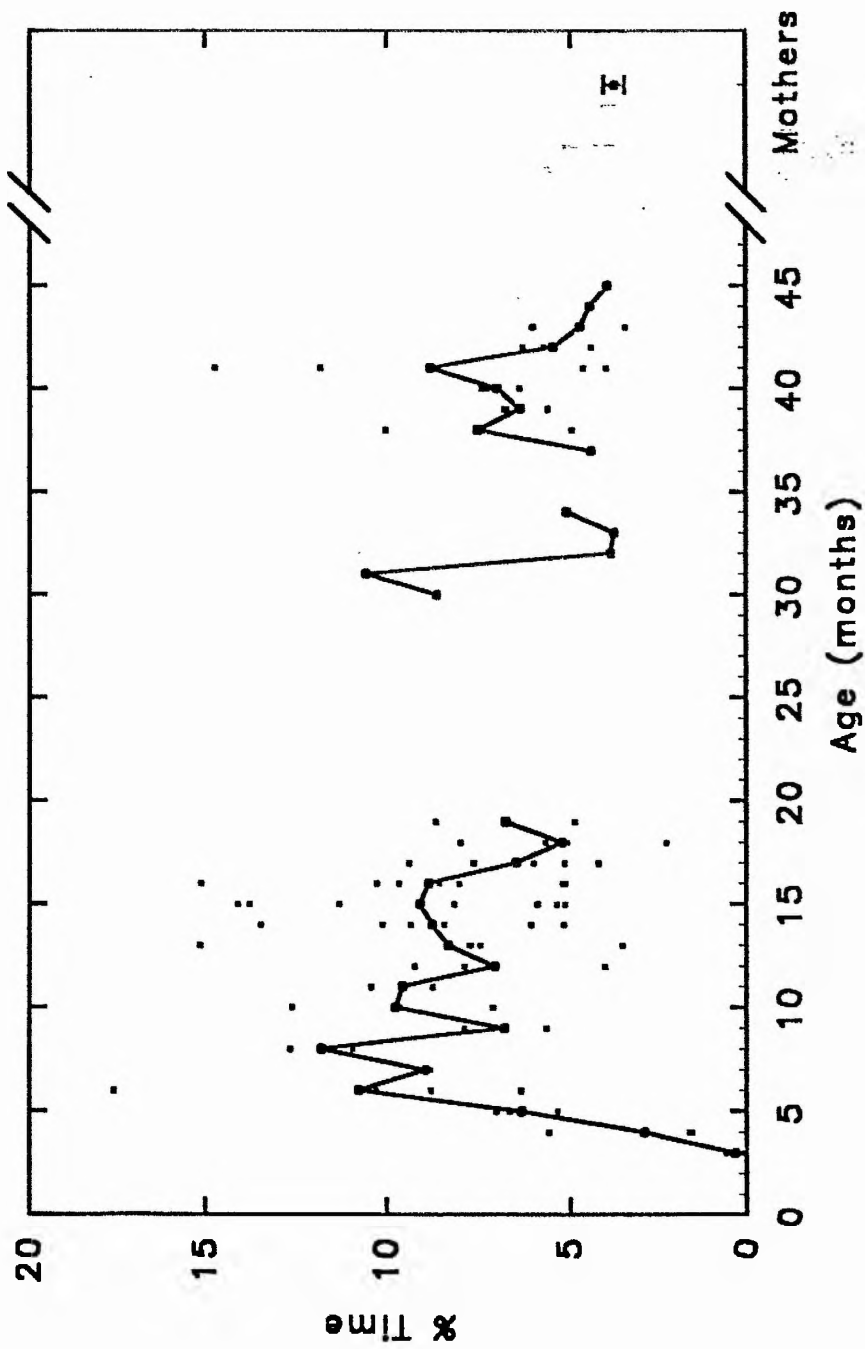


Figure 6.10: Percentage of time spent exploring for food: small solid squares represent individual data for infants and young juveniles (3 - 45 months old); open squares joined by the line represent the means of these data by age (in months). The mean value for a group of mothers is presented, with standard error bar.

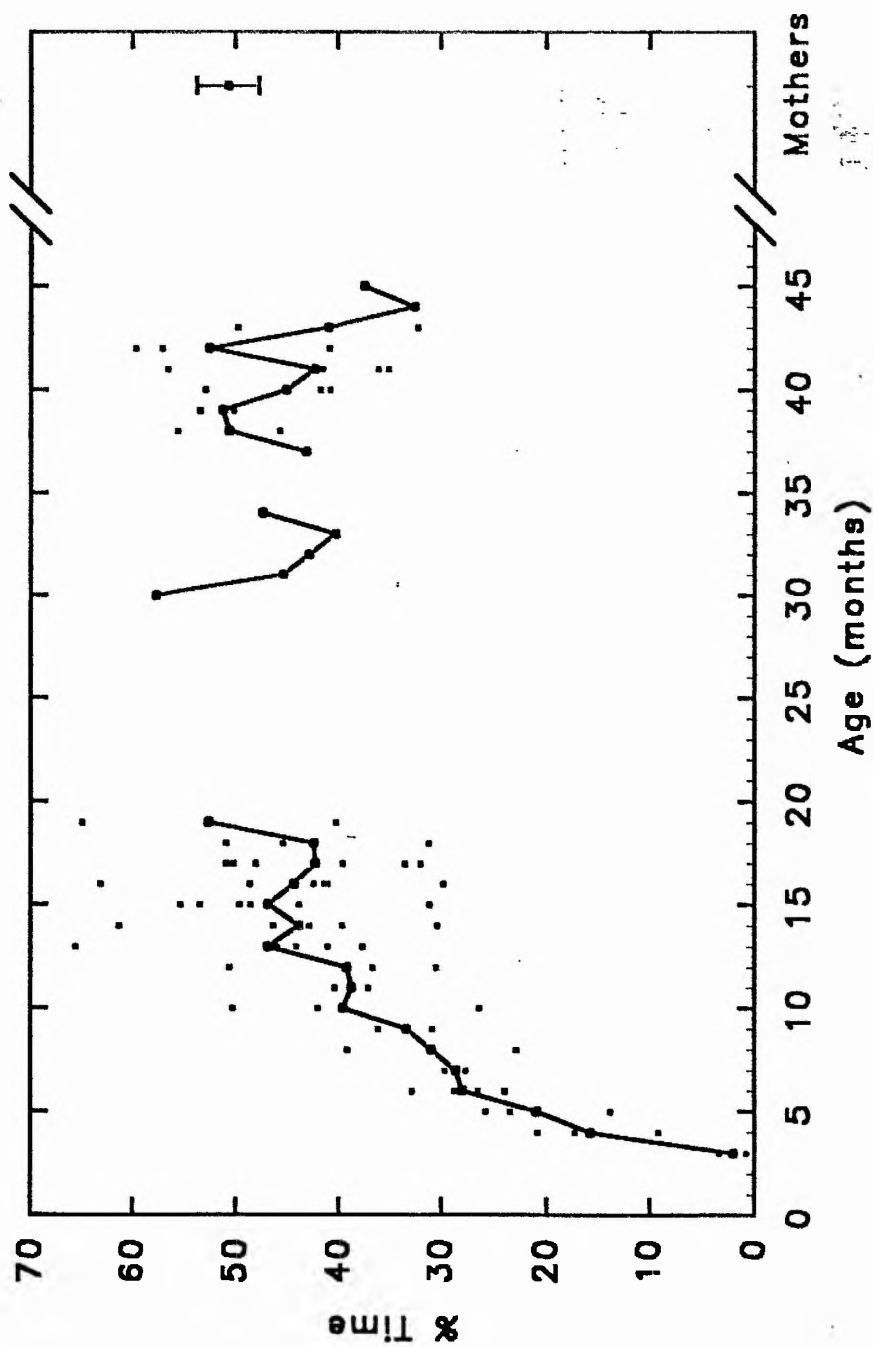


Figure 6.11: Percentage of time spent feeding: small solid squares represent individual data for infants and young juveniles (3 - 45 months old); open squares joined by the line represent the means of these data by age (in months). The mean value for a group of mothers is presented, with standard error bar.

increase in the percentage of time spent feeding on solid foods from nearly 0% at 3 months of age to a value of around 40% at 10 months old, after which age the increase in percentage of time spent feeding on solid foods was smaller. Compared with the data for other behavioural categories, the amount of variation in these data is small, especially when disregarding the values where there was only a single subject at that age. The adult female mean value for time spent feeding on solid food is 50.7% (SE = 3.0). The amount of time spent feeding varied significantly across groups of young infants, older infants, young juveniles and mothers (K-W test: $\chi^2 = 8.69$, $p = 0.034$). The amount of time spent feeding by young infants ($\bar{x} = 21.0\%$, SE = 1.1) was significantly less than that of older infants ($\bar{x} = 44.7\%$, SE = 2.7), young juveniles ($\bar{x} = 46.8\%$, SE = 2.8) and mothers (M-W U tests: $p = 0.02$, 0.034 and 0.02 respectively), though there were no significant differences in the time spent feeding for these groups.

By 10 months old infants spent a large proportion of their time feeding on solid foods. However, the transition to feeding on solid foods from feeding on milk is slow: suckling and feeding on solid foods occur in parallel for at least the first year of life (Nicolson, 1982; and see next section). Nash (1978) presents data on the amount of time subjects spent feeding alone i.e. no other animal within 60cm. Her data show a marked increase in the time spent feeding alone with increasing age, and she notes that the sharpest increase is between 10 and 13 months old. Nicolson (1982) reports that by 14 months of age, infants were spending as much time feeding as adults. The data in this study are consistent with this and show that the time spent feeding by older infants (15 - 17 months old) was not significantly different from that of adults.

Pereira (1984) presents data on the percentage of time spent feeding for his younger and older juvenile subjects, mean values of 47.5% and 43.9% respectively. These values are very similar to the values for older infants and young juveniles presented here. The difference between the data from Pereira's two age groups is significant (though note that some care should be employed when interpreting these mean data (see discussion of 'moving' earlier)). Pereira's 'feeding' category includes

grasping and manipulation of food items as well as ingestion, as opposed to the definition involving only ingestion used in this study for 'feeding'. It is likely that the higher percentage of time spent 'feeding' by Pereira's young infants is due to a larger amount of time being spent in this part of the feeding activity than on food ingestion alone.

As an infant grows older, the percentage of time spent independently ingesting solid foods increases. An infant becomes nutritionally independent i.e. weaned (see Chapter 5) by spending time environmentally exploring, exploring for food and locomoting during the first year and a half of life. Age-related change between feeding and these activities is examined in the following activity budget section.

Data from the behavioural categories 'at the nipple' and 'rejection' (see Appendix A) have already been presented and discussed in Chapter 5. The time spent in these activities is included in the activity budgets of these subjects in the next section. In summary, this section has presented data on the behavioural activities of young baboons and indicated patterns of developmental change for many of the activities. In the next section I incorporate all these behavioural activities into a complete activity budget to examine interactions between the different activities and how these change with age.

DEVELOPMENTAL CHANGE IN ACTIVITY BUDGETS

Figure 6.12(a) presents cumulatively the mean activity data for all ages, in order to generate the complete activity budget. The data are presented in the order that they were discussed in the previous section, along with data on 'at the nipple' and 'rejection'. (Note that the data for ages 30 - 34 months of age come from one individual, so should be viewed with caution.)

At 3 - 4 months old, infant subjects spent about 30% of their time at their mothers' nipple: the behaviours of environmental exploring and visually attending

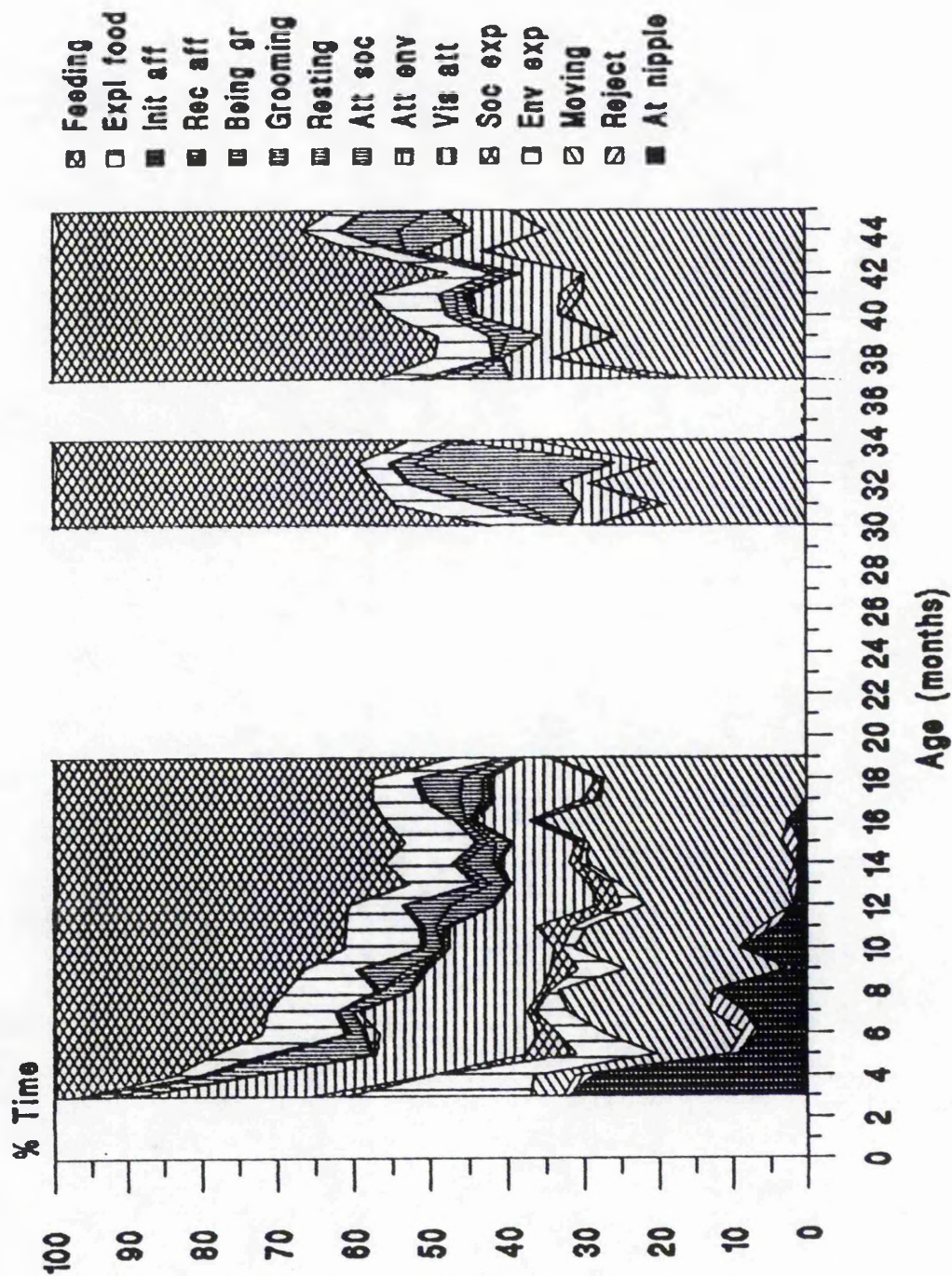


Figure 6.12(a): Activity budgets of infants and young juveniles from 3 - 45 months old presented by age (in months)

dominated the remainder of their activity budget (another 50%) with little time being spent moving independently or feeding independently and on solid foods (about 5% each). At around 10 - 12 months old, time spent at the mother's nipple was only about 5% of their time budget, and the activities of moving and feeding accounted for about 60 - 70% of their time. Time was spent exploring for food (about 10%) and visually attending (about 10%), but time spent exploring had decreased greatly. By 18 - 19 months of age, subjects no longer spent any time at their mothers' nipple, and feeding, exploring for food and moving independently accounted for more than 90% of their time budget. The remaining time was spent visually attending and in social behaviour. The activity budgets of young juvenile baboons were similar to those of the older infants, again about 80 - 90% of their activity budget was occupied by feeding, exploring for food and moving (though with fewer subjects at this age, the data show more variation).

Figure 6.12(b) represents the data for the young and older infants in this study at larger magnification, in order to examine more closely age-related changes in activity budget. Presenting the data cumulatively illustrates relationships between the behavioural activities which were described separately in the previous section and in Chapter 5. For example, the comparison between the activities of being groomed and grooming is clearly illustrated, where at 9 - 11 months old more time is spent being groomed, but from 12 months old a similar amount of time is spent grooming as this activity becomes more reciprocal. There may also be a relationship between rejection and time spent at the nipple, where the large amount of time spent being rejected at 6 - 7 months was followed by increased time spent on the nipple at 8 months of age.

These data suggest possible interactions between time spent in different activities: when more time is spent in one activity, less time is (or must be) spent in another. To examine these interactions, these mean values of time spent in each behavioural activity were correlated with those for all other activity categories for infant subjects at each age (in months) ($N = 17$, $df = 15$). Only values of the Pearson correlation coefficient greater than 0.7 were considered (i.e. the strongest correlations,

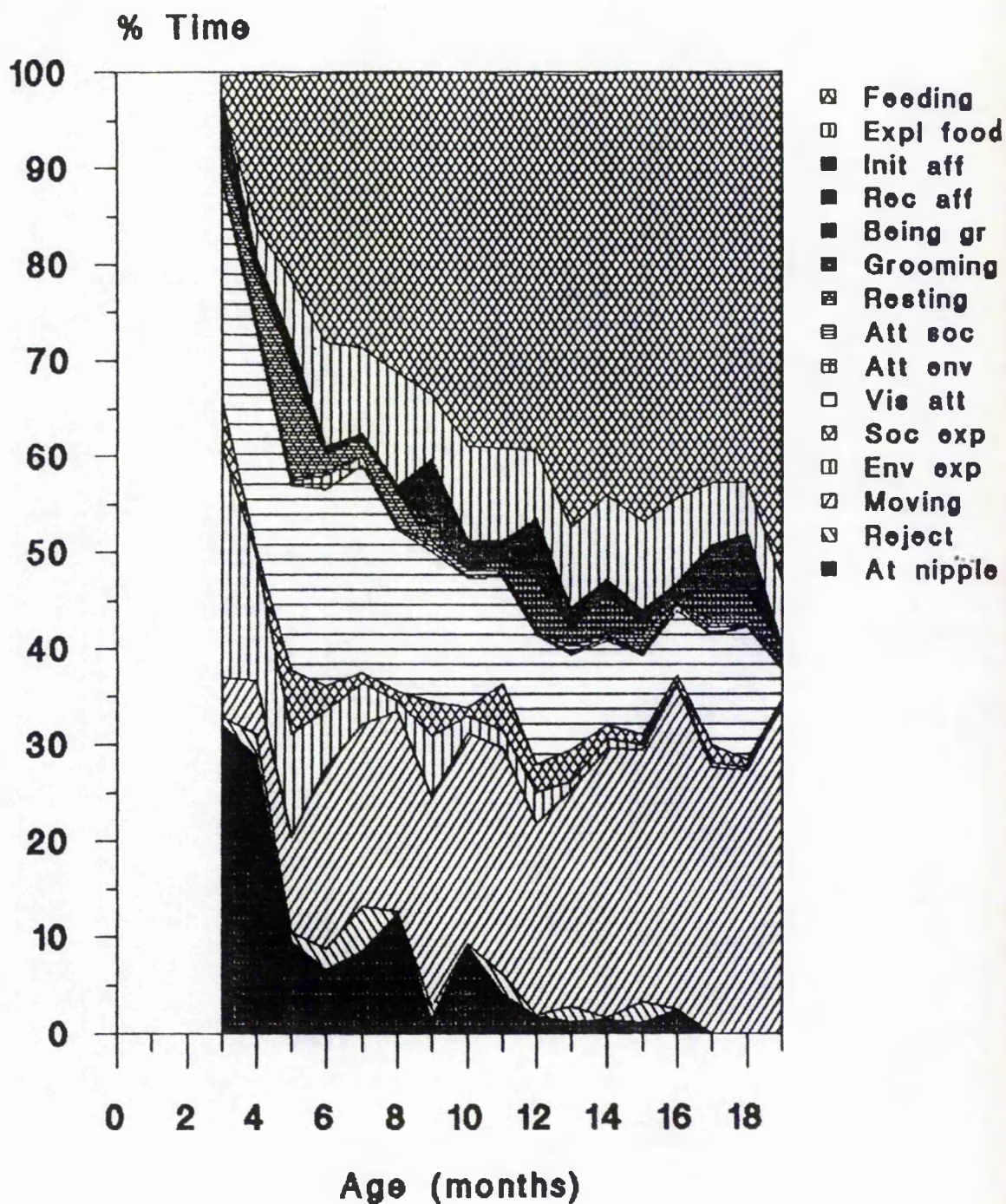


Figure 6.12(b): Activity budgets of infants from 3 - 19 months old presented by age (in months)

and where at least 50% of the variance (R^2) is explained). Table 6.2 presents these values.

There is a strong positive correlation between the percentages of time spent moving and feeding ($R = 0.93$). Similar positive correlations were found between time spent in the activities of at the nipple, environmental exploring, visually attending and receiving affiliative approaches. Time spent in each of these behavioural activities correlated negatively with the time spent moving and feeding. The amount of time spent environmentally exploring also negatively correlated with the time spent exploring for food, but this activity was not strongly correlated with other activities. The nature of these correlations is illustrated diagrammatically in Figure 6.13, which clearly shows the two groups of positively correlated behavioural activities and their negative relationship with each other. As age increased and time spent moving increased, more time was also spent feeding, but less time was spent at the nipple, environmentally exploring, visually attending and receiving affiliative approaches. Nicolson (1982) reports that an infant obtains nourishment from both suckling and feeding on solid foods during the first year but that the amounts of time spent in these activities are negatively correlated, and that time spent moving independently is negatively correlated with the time spent riding on the mother. The correlations on time spent moving, feeding and at the nipple presented here are therefore consistent with these results and demonstrate the acquisition of nutritional and locomotory independence (see also Chapter 5). Further, these correlations describe in more detail related changes in behaviour during this acquisition of independence: the associated decline in visually attending, environmentally exploring and receiving affiliative approaches.

Another interaction which has become clear is the relationship between visually attending and moving. The time spent visually attending was high for very young infants while the time spent travelling independently was low: much visually attending therefore seems to occur when infants are riding dorsally on their mothers, but then the time spent in this activity decreases as infants spend more time moving independently.

I make no claims for the causality of the changes in activity budget behaviour

Table 6.2: Pearson's correlation coefficient (R) values greater than 0.7, from the correlation of the percentage of time spent in each activity with that spent in all other activities. (N = 17) ¹

	FEEDING	AT NIPPLE	ENVIRONMENTAL EXPLORING	VISUALLY ATTENDING	RECEIVING AFFILIATIVE APPROACHES
MOVING	0.93	-0.85	-0.88	-0.88	-0.88
FEEDING	---	-0.90	-0.93	-0.90	-0.95
AT NIPPLE		---	0.87	0.74	0.79
ENVIRON. EXPLORING			---	0.74	0.85
VISUALLY ATTENDING				---	0.88
* exploring for food R = -0.74					

¹ All correlations significant at $p = 0.05$

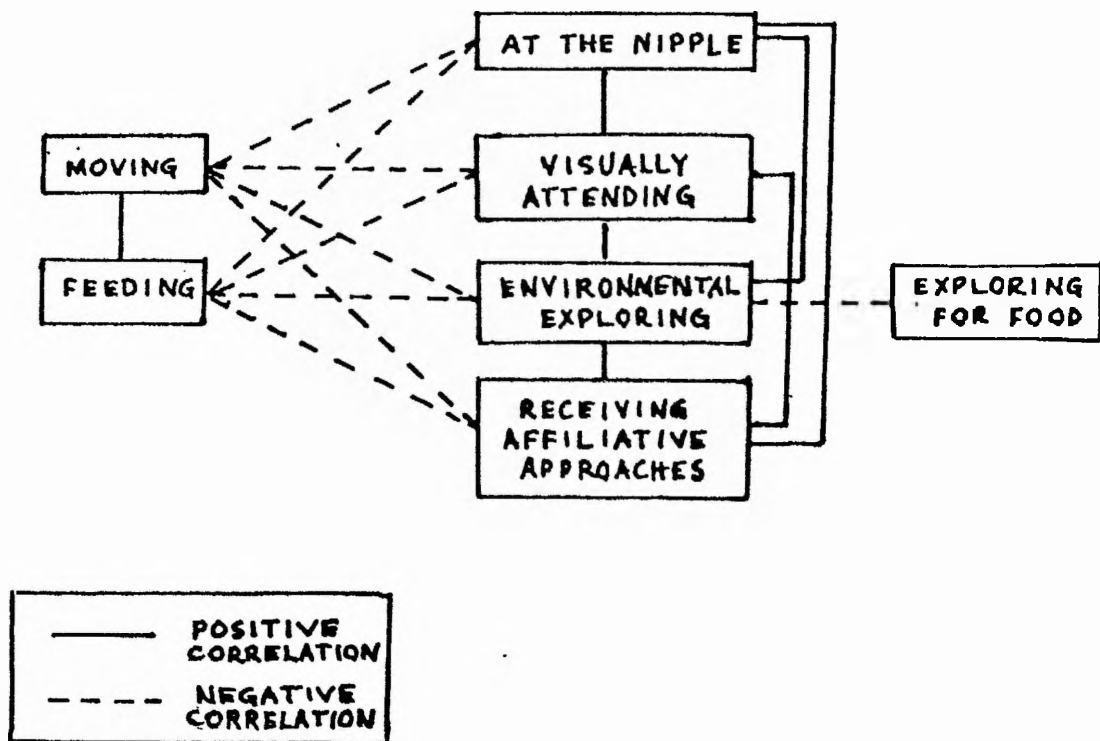


Figure 6.13: Diagrammatic representation of the correlations between behavioural activities where Pearson's correlation coefficient, $R > 0.7$.

discussed here. It is not possible to say which behaviour is driving these changes.

CONCLUSIONS

This chapter has presented data on the amount of time infant and young juvenile baboons in this troop spent in various activities. In the last section, the data on percentage of time spent in behavioural activities were compiled to form a complete and detailed activity budget of this age group, and this was then discussed with respect to age-related changes. Few previous studies of infants and juveniles have presented such data, or shown the age-related change that occurs in these behavioural activities.

The patterns of behavioural change shown in this chapter reflect infants' change in behaviour during the acquisition of independence, from that when he is able to rely on his mother for nutrition and locomotion when young, to that when he is independent from her by the start of the second year. For some behavioural activities e.g. moving, the time spent in that activity by older infants is already similar to that of adults; however, for behavioural activities such as socially exploring, the time course of development is longer.

Clearly from the work presented in this chapter, there are age-related changes in the behaviour of young baboons. Although in the past "students of kinship, altruism and competition [i.e. social behaviour] tended to disregard age as an independent variable, perhaps because few had enough information to consider fairly how it modulates behavioural selection and expression" (Pereira and Fairbanks, in press), when studying the behaviour of this age group, developmental changes in behaviour **MUST** be taken into account before examining effects such as those of environmental change. This chapter has therefore presented descriptions of the behaviour of young baboons which acts as the context within which to examine the effect of other variables such as seasonal fluctuations in food availability on behaviour. This will be done in the following chapter.

CHAPTER 7: THE EFFECT OF SEASONAL STRESS ON THE BEHAVIOUR OF YOUNG BABOONS

INTRODUCTION

This thesis has presented data which show that at Cholulu, there are seasonal fluctuations in rainfall and the availability of food resources. The ranging behaviour of the troop as a whole has been related to food availability, and differential use of the home range area and sub-trooping behaviour have been discussed as adaptive behavioural strategies for living in this seasonal environment. The activity budgets of infants and young juveniles have been presented, and developmental changes both in the behaviour associated with the mother-offspring relationship, and in behavioural activities, have been demonstrated and discussed. Finally, in this chapter, I examine the impact of seasonal fluctuations in food availability on the behaviour of these young baboons.

As well as experiencing seasonal environmental fluctuations, individuals in this age group are developing and acquiring independence, so there is a potentially complex interaction between the effects of development and seasonality on behaviour. In order to examine the effect of seasonal fluctuations on behaviour, it is therefore important to determine the variation in behaviour which is associated with development, and then to analyse the remaining variation for the effects of other factors, of which seasonality is likely to be one.

When examining the effect of time spent feeding on gestation length in female baboons, where amount of recent rainfall influenced feeding behaviour and therefore also gestation length, Silk (1986) computed a regression equation between rainfall and time spent feeding and used this to provide a baseline prediction of the proportion of time a female would spend feeding on a given day; she then calculated residual values for individuals' proportion of time spent feeding to examine their deviation from the expected value, i.e. she subtracted the effect of rainfall from the variation in behaviour.

In this study of young baboons, a similar technique of examining residuals was developed, where the variation in behaviour associated with development (demonstrated in Chapters 5 and 6) was held constant as the baseline, and individuals' residual values for proportions of time spent in various activities were then examined with respect to food availability.

The development and details of this technique are presented below, and the results of analyses for the amount of time spent in the activities associated with the mother-offspring relationship, and for the time spent in the behavioural activities described in Chapter 6, are presented in the following sections. Individual differences in the timing and nature of weaning are also related to food availability. Finally data on seasonal variation in the diet of young baboons are presented. In the concluding section, the implications of this research are discussed, and ideas for further analysis and research are suggested.

ADDITIONAL NOTES ON METHODOLOGY

In order to examine residuals from baseline developmental change in each behavioural activity, a curve or line which represents the relationship between development and the behaviour must be found. Change in behaviour which is associated with development is likely to follow some form of exponential course (simple or complex, positive or negative), where an asymptotic value is reached before or at adulthood. Lines which do not asymptote, e.g. straight line regressions and quadratic equations, are not likely to be appropriate models to use for this type of behaviour. Altmann (1980) presents plots of residuals where a linear regression was fitted to data for time spent in contact with the mother: the non-random distribution of points shows that the fit was poor for the first month and after the eighth month.

In order to investigate which curve would be most appropriate to use to describe developmental change in behaviour, several different curves were fitted to the data for percentage of time spent moving, using the computer package 'SIGMAPLOT'. First,

an exponential equation of the form $y = a - be^{-kx}$ was examined, where x = age in months and y = percentage of time spent in the activity. Behaviourally, when age is zero, time spent moving must be zero, so the equation was constrained to pass through the origin ($a = b$). The resulting curve is illustrated in Figure 7.1(a). 'SIGMAPLOT' calculates goodness of fit from the square root of the sum of the square of the residuals and represents this as a 'Norm' value: a lower 'Norm' indicates a better fit. For this equation, 'Norm' was 31.59. Inspecting the plot by eye, while the equation fitted the data from older subjects well, it is a relatively poor fit for the younger subjects. A slightly better fit was obtained by not constraining the exponential ('Norm' = 30.44, and see Figure 7.1(b)); however, this equation lacked behavioural meaning because of not passing through the origin. This equation suggests, however, that a curve which increases from the origin at a slow rate, then at a faster rate, and finally at a slower rate before reaching an asymptote (i.e. a sigmoid shape), would describe these data better.

Zullinger et al. (1984) show that mammalian growth curves are sigmoidal in shape (see also Chapter 5: Introduction), where rate of change is slow, increases to a faster rate, and then decreases as the asymptote is reached. They chose the Gompertz sigmoid equation $y = ae^{-e^{-k(x-i)}}$ as a standard to enable interspecific comparisons for growth. Following Zullinger et al., Rasmussen and Tan (in press) fitted Gompertz sigmoid curves to behavioural data on rates of suckling and physical independence, in order to provide a basis for interspecific comparisons (although they also suggested that such a technique could perhaps be used to illuminate environmental effects on intra-specific variation). A Gompertz equation constrained to pass through the origin was therefore considered as a model for developmental change for the broader range of behavioural activities that were used in this study. (Other sigmoid equations, e.g. von Bertalanffy's, were examined for their appropriateness to model developmental behavioural change, but were rejected because when constrained to pass through the origin, the curve became a simple exponential rather than sigmoidal, and when unconstrained the curve cuts the y axis at a negative value, which would be

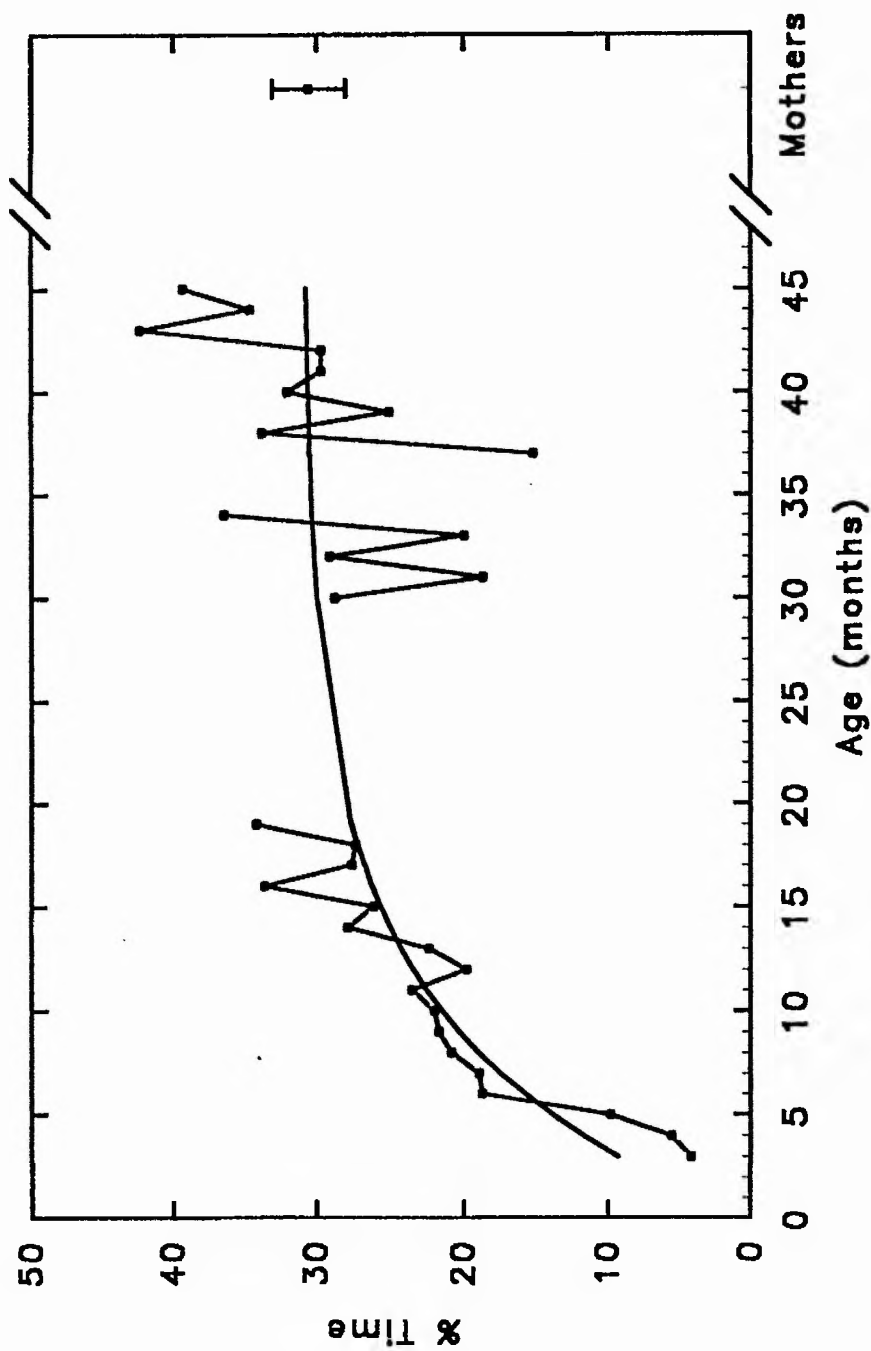


Figure 7.1(a): Curve from an exponential equation of the form $y = a - be^{-kx}$ constrained to pass through the origin ($a = b$), fitted to the mean data for percentage of time spent moving.

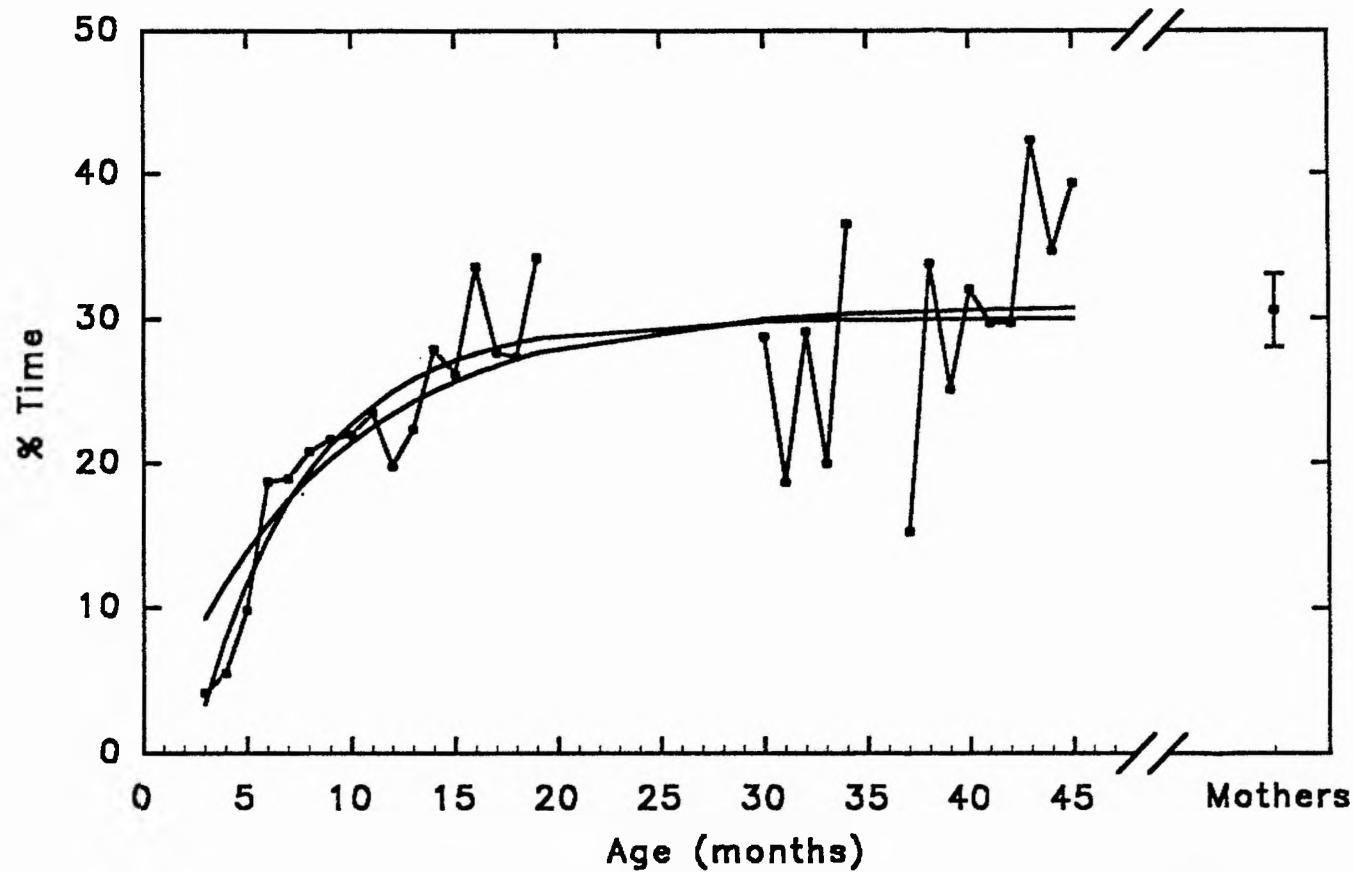


Figure 7.1(b): Curve from an exponential equation of the form $y = a - be^{-kx}$ not constrained to pass through the origin compared with a curve from the same exponential equation constrained to pass through the origin (Figure 7.1(a)), fitted to the mean data for percentage of time spent moving.

behaviourally meaningless.) This equation fitted to the data for percentage of time spent moving attained a 'Norm' value of 30.68 (see Figure 7.1(c)). An equation which would obtain a lower 'Norm' value could be generated by using a more complex equation (in an extreme case, passing through each data point), but this is unlikely to be behaviourally meaningful. For this study, the Gompertz sigmoid equation was considered to be a useful model to fit to behavioural data in order to provide a baseline for developmental change.

For each behavioural activity, if the mean data presented in Chapters 5 and 6 showed a significant difference between the behaviour of groups of young infants, older infants, juveniles and mothers, one of several types of curve based on the Gompertz sigmoid equation was fitted to these data; the choice of curve to be fitted was dictated by the nature of the behavioural activity as follows:

(i) For the behavioural activities 'moving', 'feeding', and 'grooming', when age is zero, the percentage of time spent in these activities is zero. This amount of time then increases with increasing age until an adult level is reached. A positive Gompertz sigmoid curve through the origin (illustrated in Figure 7.2(a)) was therefore selected for these activities. Figure 7.3 presents this sigmoidal curve fitted to the data on percentage of time spent feeding. (The lack of data for < 3 months old means the first part of the curve is missing.)

(ii) For time spent in contact with the mother and within 5m of her, time spent 'at the nipple' and time spent 'visually attending', values are high in the first weeks of life and then decline as age increases, so a negative Gompertz sigmoid curve (illustrated in Figure 7.2(b)) was fitted to these data. Figures 7.4(a) and (b) present the curves fitted for time spent in contact with the mother and time spent 'visually attending'.

(iii) With the behavioural activities 'environmental exploring', 'social exploring', 'exploring for food' and 'receiving affiliative approaches', when age is zero, the amount of time spent in these activities must be zero (since they all require mobility and coordination which is lacking for the first few weeks of life); however, the time spent in these activities then increases, in some cases very rapidly, a peak level is

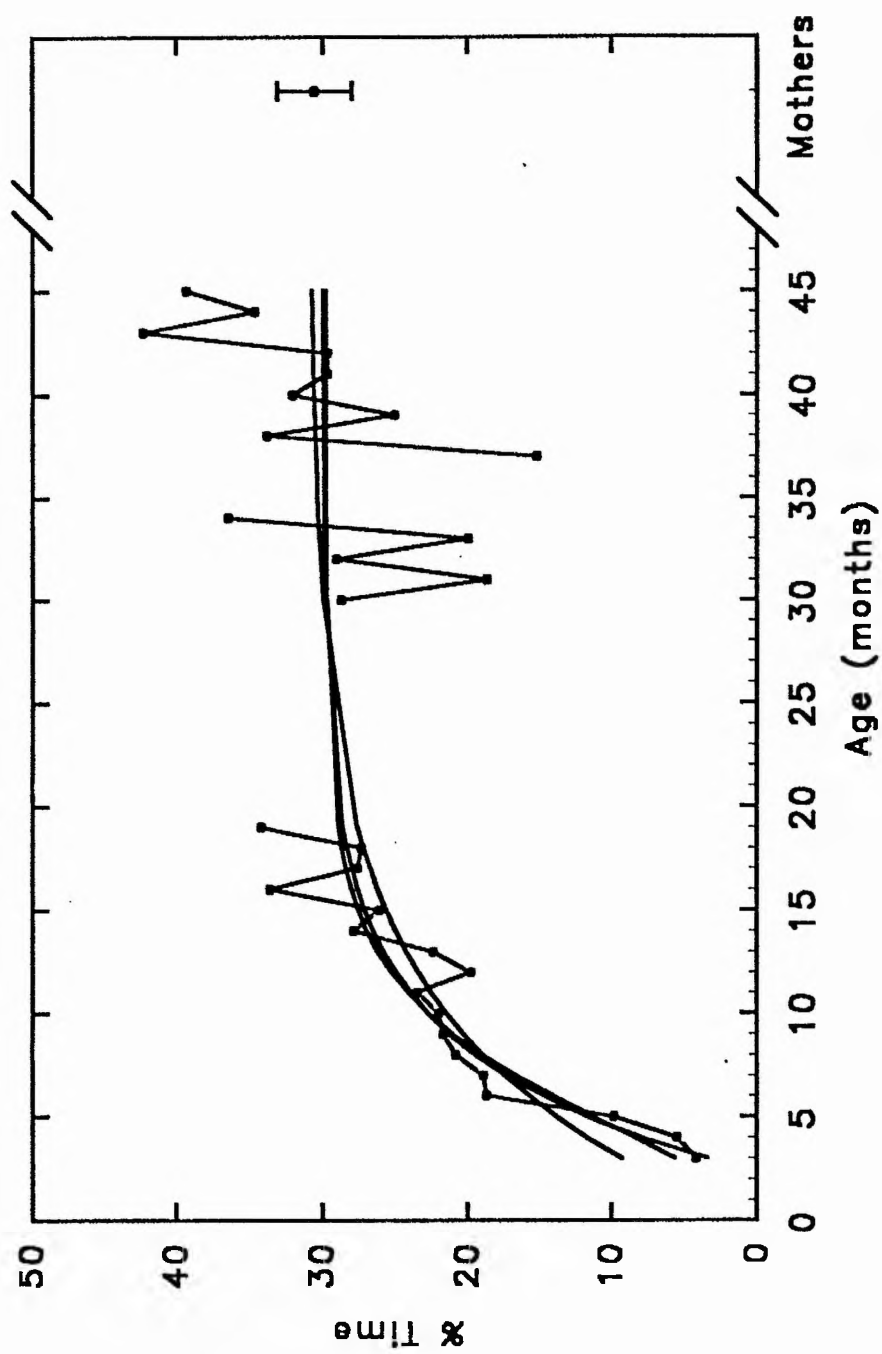


Figure 7.1(c): Comparison of a curve from the Gompertz sigmoid equation $y = ae^{-e^{-k(x-l)}}$ constrained to pass through the origin with curves from the exponential equation (Figure 7.1(b)), fitted to the mean data for percentage of time spent moving.

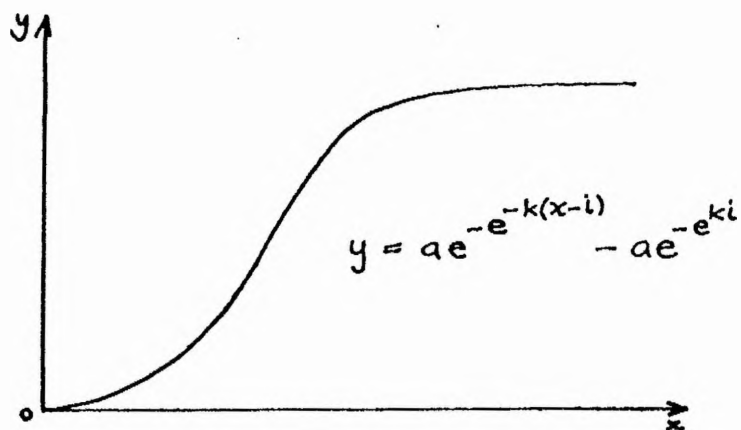


Figure 7.2(a): Shape of a positive Gompertz sigmoid curve through the origin.

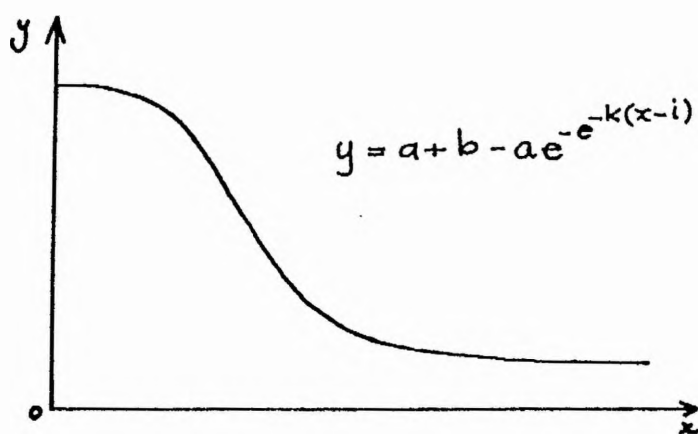


Figure 7.2(b): Shape of a negative Gompertz sigmoid curve.

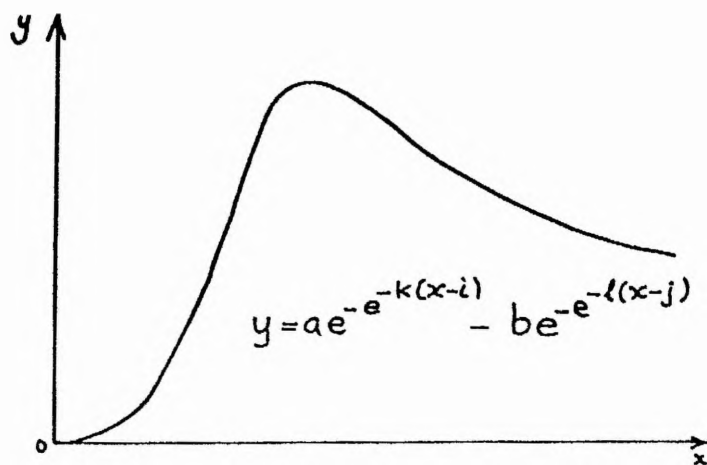


Figure 7.2(c): Shape generated by the difference between two Gompertz sigmoid curves.

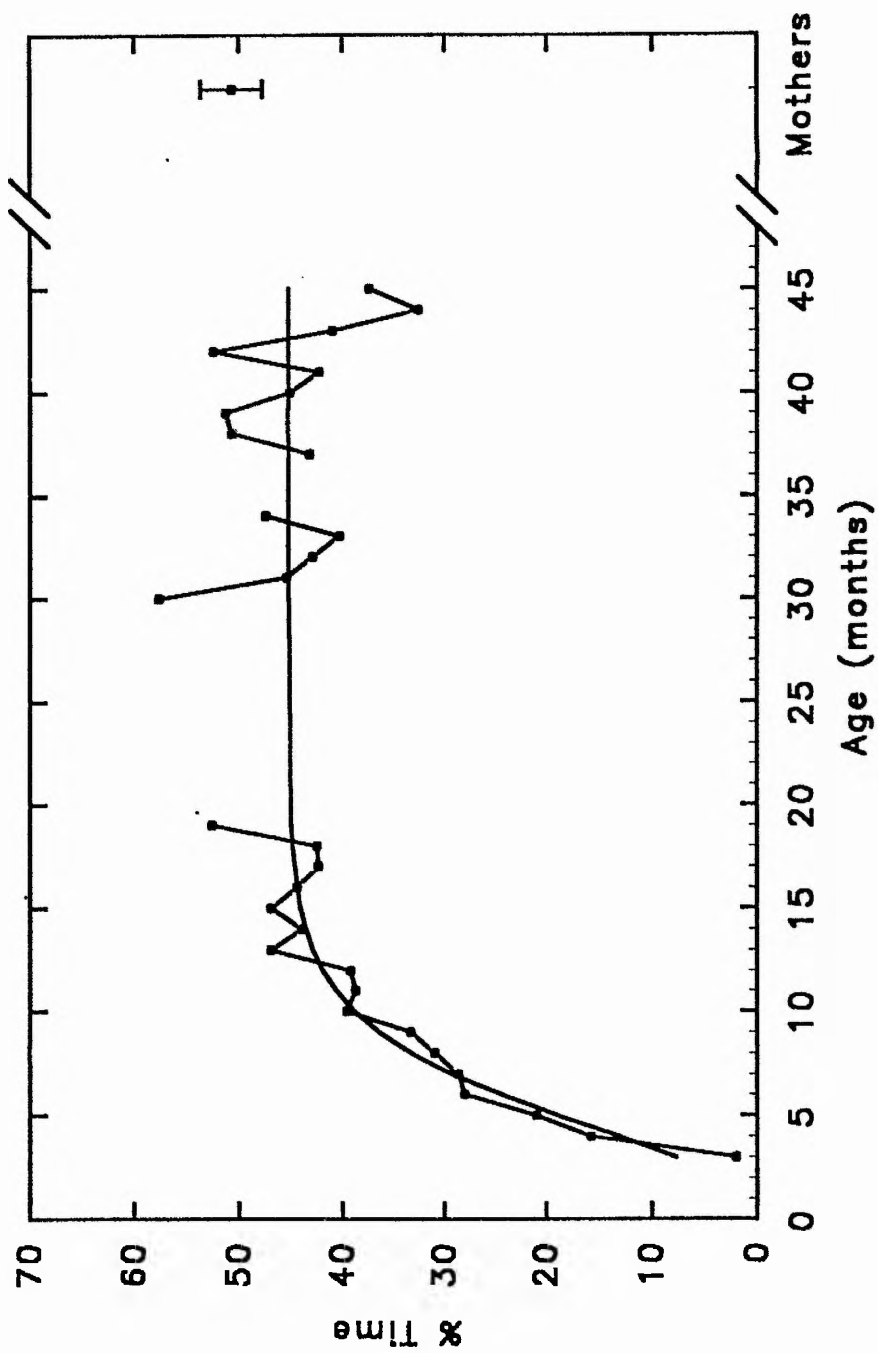


Figure 7.3: Mean percentage of time spent feeding presented by age (in months), with a positive Gompertz sigmoid curve through the origin fitted to these data.

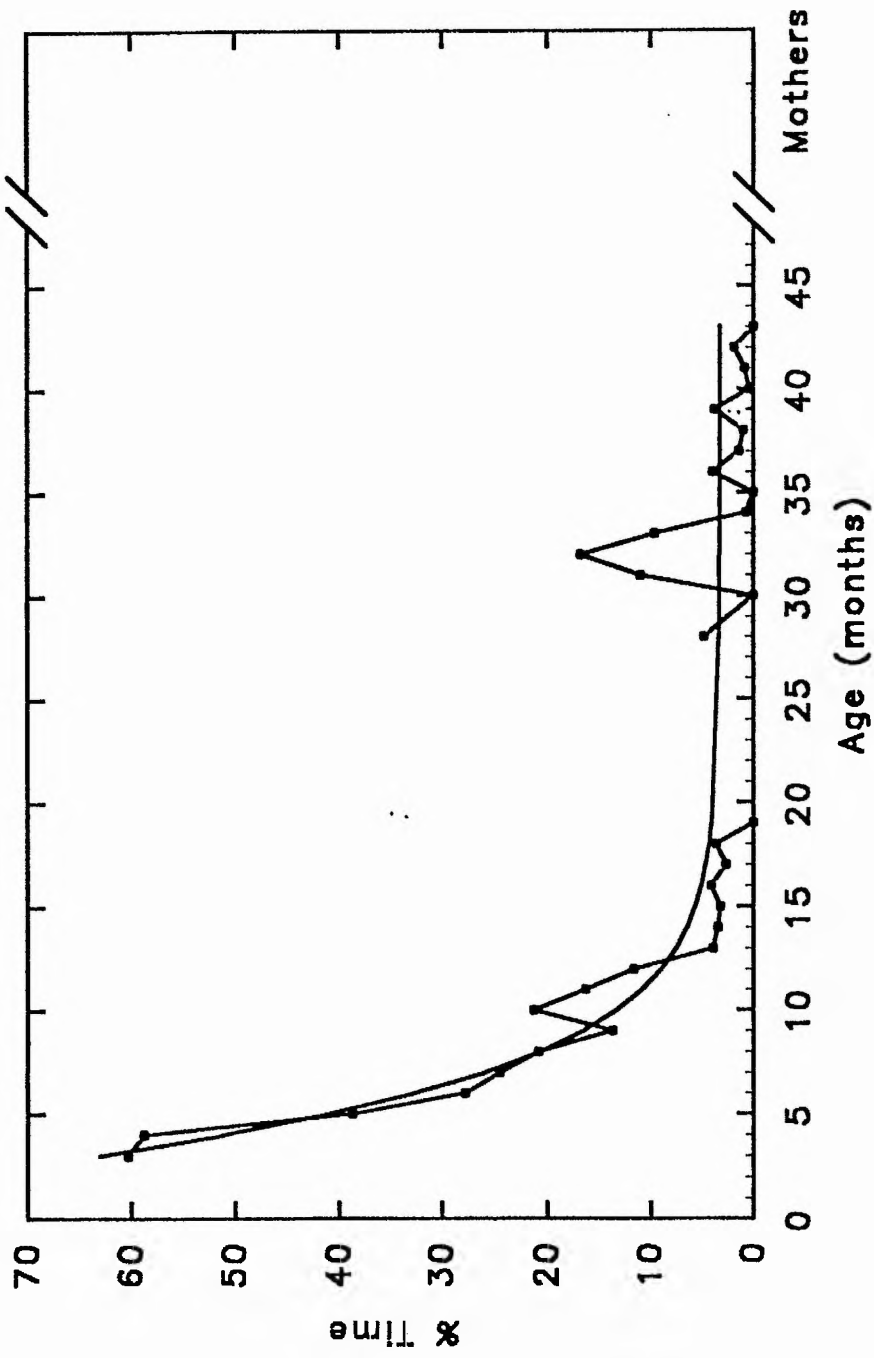


Figure 7.4(a): Mean percentage of time spent in contact with the mother presented by age (in months), with a negative Gompertz sigmoid curve fitted to these data.

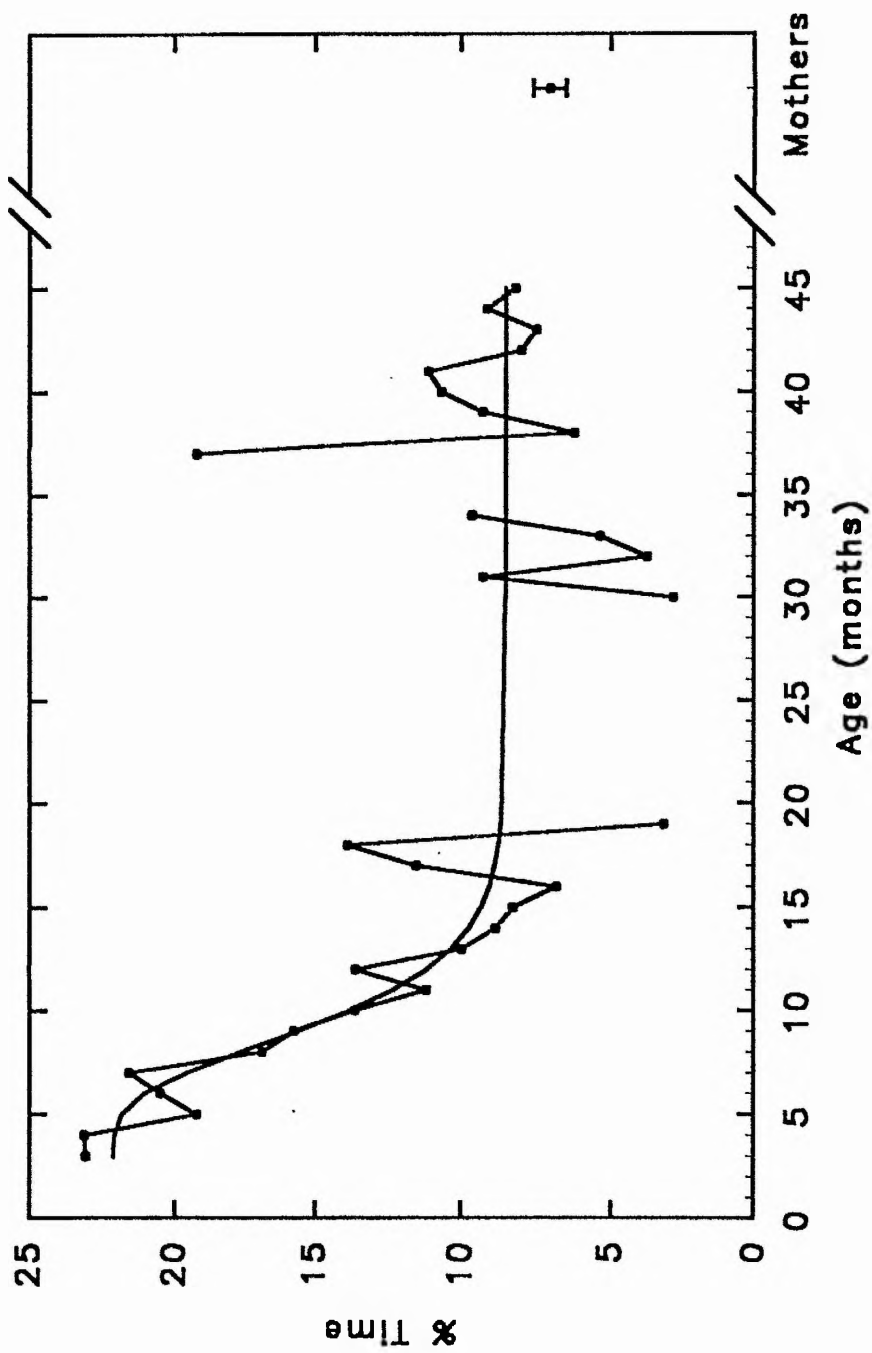


Figure 7.4(b): Mean percentage of time spent visually attending presented by age (in months), with a negative Gompertz sigmoid curve fitted to these data.

reached, and this is then followed by a decline in the amount of time spent in these activities which is usually rather more gradual than the increase. In these cases the equation for the difference between two Gompertz sigmoid curves illustrated in Figure 7.2(c)) was fitted, where one sigmoid curve has a fast rate of increase to its asymptotic value and the other has a slower rate of increase: subtracting the second curve from the first results in the shape of curve described above. In these behavioural activities, it is plausible that there are two processes going on: one which results in the sharp increase in time spent in the activity from zero at birth to a peak value which may occur within the first few weeks or months of life (perhaps to do with acquiring physical dexterity), and the other (perhaps to do with learning and experience) which governs the slower decline in the time spent in these activities. Figures 7.5(a) and (b) present the curves fitted to the data for 'exploring for food' and 'environmental exploring'. In Figure 7.5(b), the rate of increase occurred very rapidly, and at an age earlier than those for which data are available.

Using mean data (presented in Chapters 5 and 6) to fit curves for each behavioural activity, values where only one individual contributes to the mean can have a disproportionate influence on the shape of the curve fitted. This is clearly illustrated by the curve fitted to the mean data for time spent grooming (Figure 7.6), and is also obvious in the curves for time spent in close proximity to the mother. In most cases, however, the values where only one subject contributes to the mean (particularly at 30 - 34 months of age) are not very different from the neighbouring values, so the effect on the resulting curve is less influential. By 30 months of age, the curves generally have reached their asymptotes, so for the comparison of residuals, the actual value of the asymptote is relatively unimportant.

Once a curve has been fitted to the data to represent baseline developmental behaviour (i.e. once variation in behaviour associated with development has been accounted for) (see Figure 7.7(a)), the residuals from individual data points to the curve can be calculated (see Figure 7.7(b)). Plots of these residuals by age, assessed by eye, indicate that there is no pattern of autocorrelation.

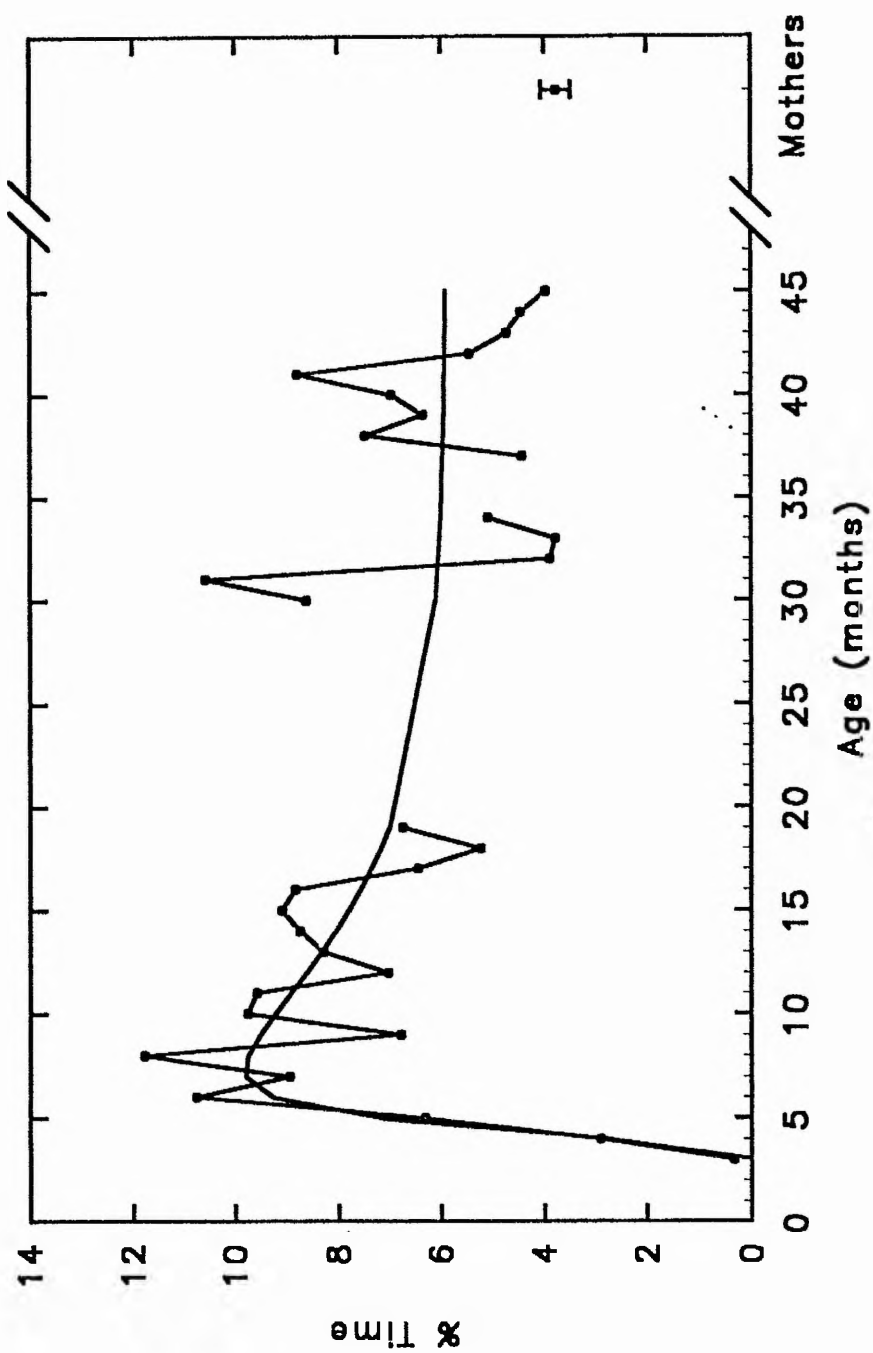


Figure 7.5(a): Mean percentage of time spent exploring for food presented by age (in months), with the equation for the difference between two Gompertz sigmoid curves fitted to these data.

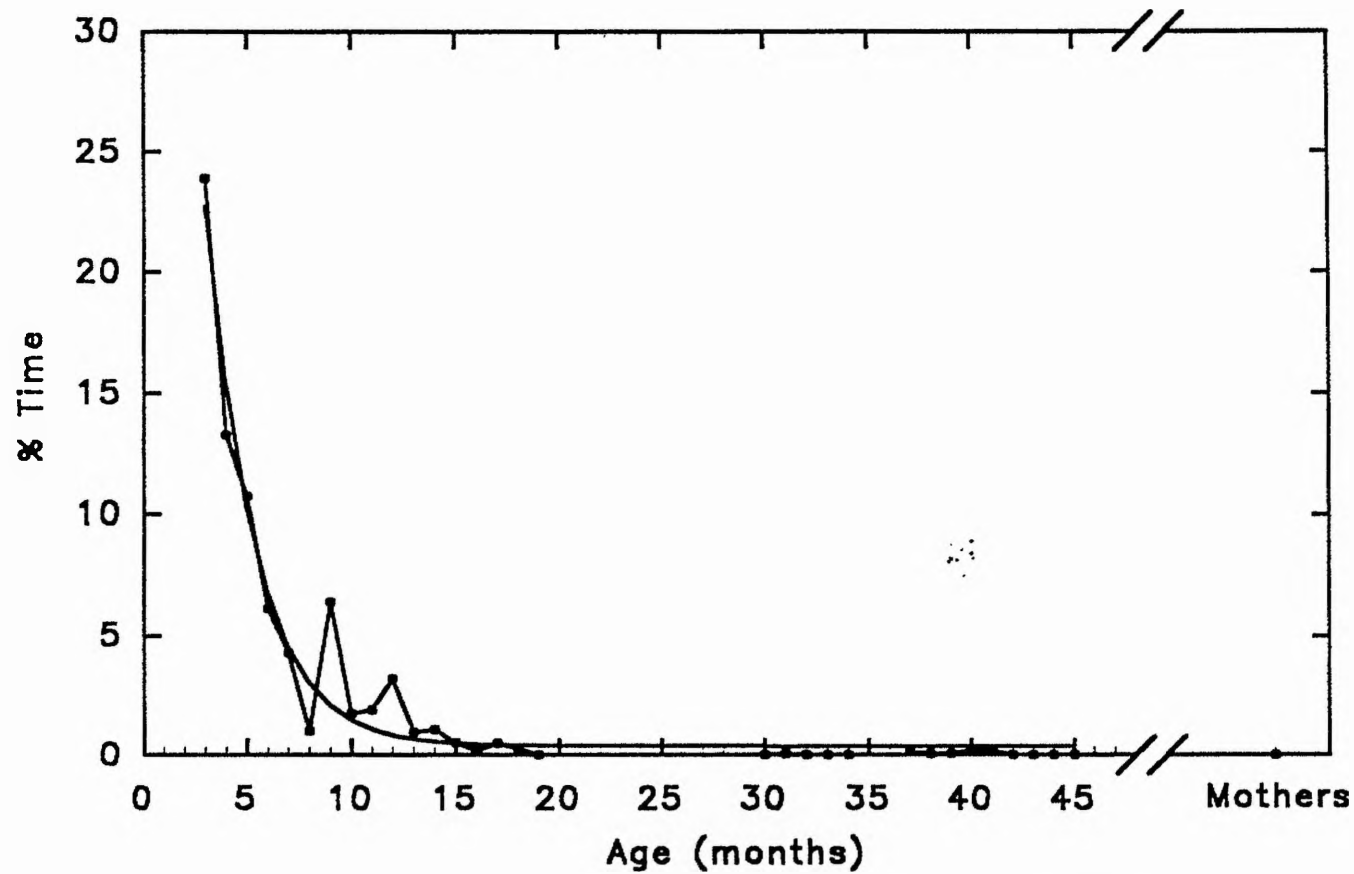


Figure 7.5(b): Mean percentage of time spent environmentally exploring presented by age (in months), with the equation for the difference between two Gompertz sigmoid curves fitted to these data.

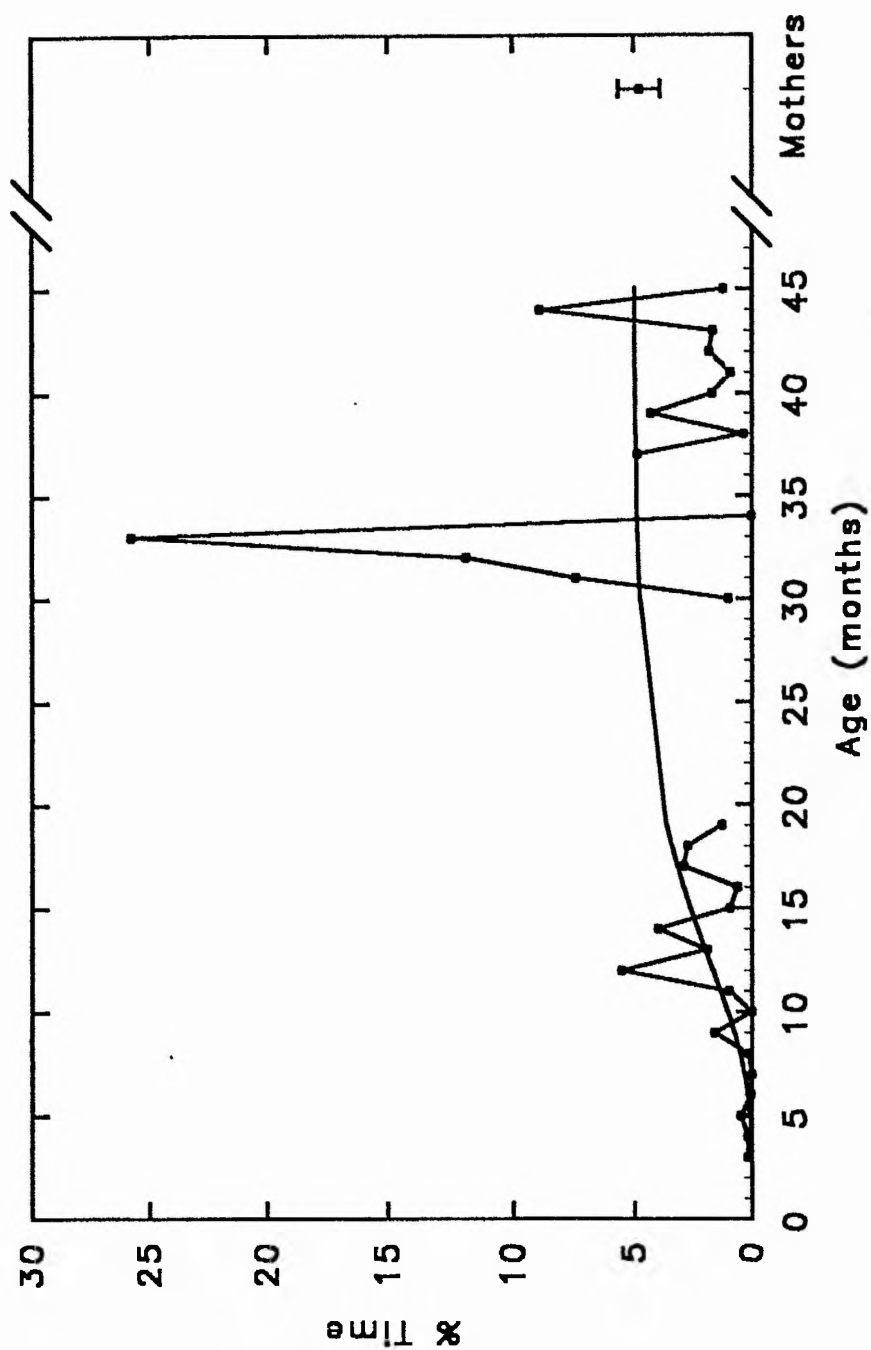


Figure 7.6: Mean percentage of time spent grooming presented by age (in months), with a positive Gompertz sigmoid curve through the origin fitted to these data. From 30 to 34 months of age, only one individual contributed to the mean value: these values therefore have a disproportionate influence on the shape of the curve fitted.

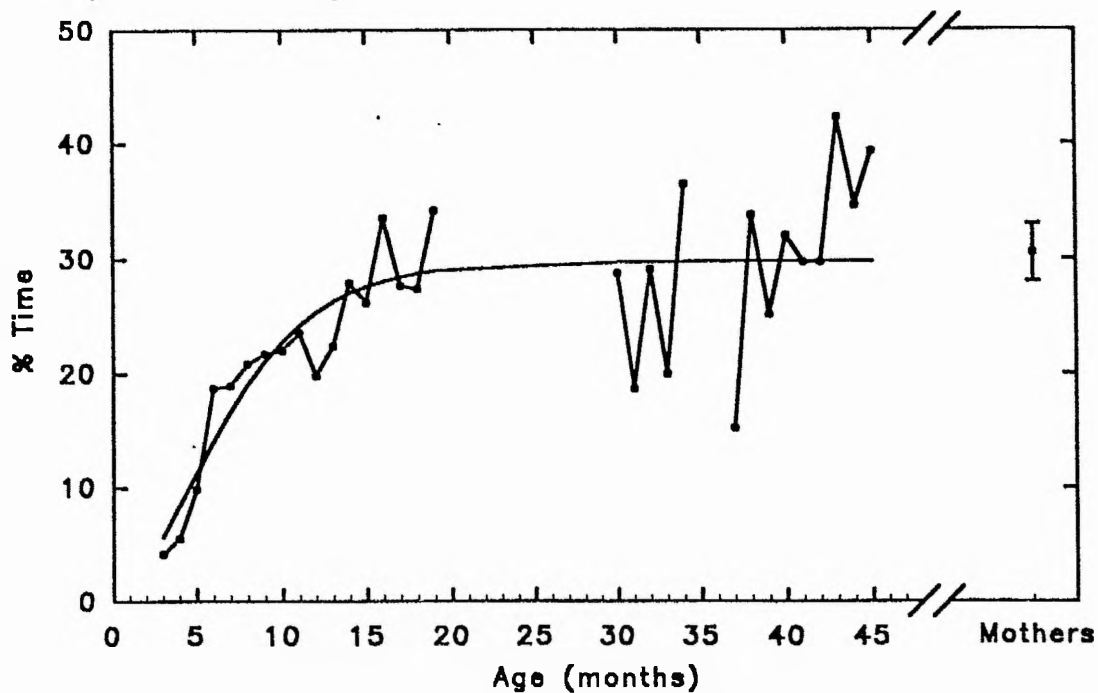


Figure 7.7(a): Positive Gompertz sigmoid curve through the origin fitted to the mean percentage of time spent moving, in order to account for the variation in behaviour associated with development.

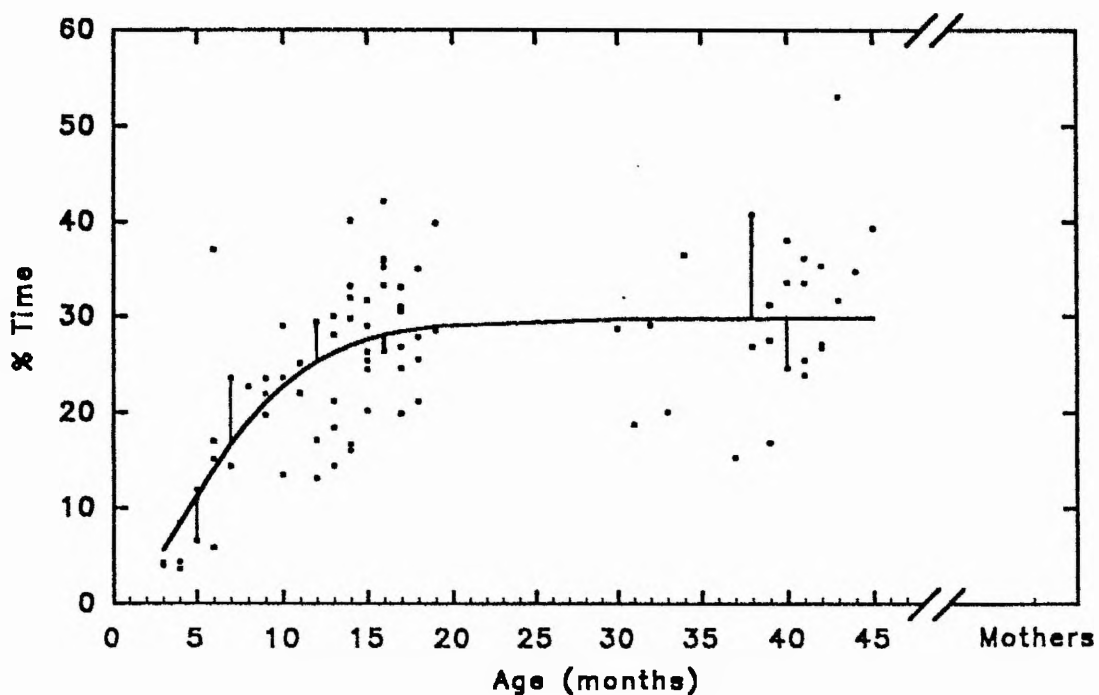


Figure 7.7(b): Residuals from individual data points to this curve.

In the case of the behavioural activities 'initiating affiliative approaches', 'being groomed', 'attending environmental' and 'attending social', there was no significant change in the amount of time spent in these activities with increasing infant and juvenile age (see Chapter 6), so it was not necessary to fit a curve to isolate the effects of development, or to calculate residuals: individuals' actual data values were used instead of residuals in the subsequent seasonality.

The mean values for each subject's residuals (actual data for the activities mentioned above) were calculated for August - October, the months of 'best' food availability within the period of focal data collection, and for May/June - July, the months of 'worst' food availability within this period, where these food availability categories were based on values of baboon food biomass data presented in Chapter 3 (Figure 3.16). These values were compared using paired T-tests across all subjects, and separately for young infants, older infants and young juveniles.

EFFECTS OF SEASONAL FOOD AVAILABILITY ON THE RELATIONSHIP BETWEEN MOTHERS AND THEIR OFFSPRING

At the nipple, contact and proximity:

Table 7.1 presents the results of the paired T-tests for the percentage of time spent at the nipple, in contact with the mother and within 5m of her, in the worst and best months. In an analysis with all subjects combined, none of the categories showed a significant difference in behaviour between the worst and best months.

By 18 months of age, all individuals were nutritionally independent (see Chapter 5): young juveniles consistently spent 0% of their time 'at the nipple', and thus would not be expected to show any seasonal effects in that activity. However, although the differences were not significant, both young infants and older infants spent less time at their mother's nipple in the worst months than in the best months, suggesting that in months of low food availability, the time these infants spent suckling was perhaps

Table 7.1: Paired T-tests for the percentage of time spent at the nipple, in contact with the mother and within 5m of her, in the worst and best months.

		Worst	Best	t	df	p
At the Nipple:	ALL SUBJECTS	-0.46	0.36	0.90	16	0.383
	YOUNG INFANTS	-0.65	0.56	0.48	5	0.651
	OLDER INFANTS	-0.28	0.84	1.05	5	0.342
	JUVENILES	-0.46	-0.46	1.23	4	0.286
In Contact with Mother:	ALL SUBJECTS	-1.28	-0.93	0.26	15	0.795
	YOUNG INFANTS	0.12	-1.76	0.61	5	0.568
	OLDER INFANTS	-2.77	-1.04	1.04	5	0.360
	JUVENILES	-1.15	0.47	2.27	3	0.108
Within 5m of Mother:	ALL SUBJECTS	-1.44	-0.02	0.68	15	0.509
	YOUNG INFANTS	1.38	-2.75	-1.10	5	0.321
	OLDER INFANTS	-3.32	2.12	1.69	5	0.152
	JUVENILES	-2.85	0.90	4.33	3	0.023*

* $p < 0.05$

decreased.

Data from the contact and proximity categories indicate a different pattern of behaviour. For the percentage of time spent in contact with and within 5m of the mother, there is the suggestion that young infants spent more time in contact with and close proximity to the mother in the worst months than in the best months, while older infants and young juveniles (who still spent some time in contact with and close proximity to the mother: see Chapter 5) spent less time in contact with and within 5m of the mother in the worst months compared with the best months. For young juvenile subjects, there was a significant difference between the mean value for worst months and the best months ($df = 3$, $p = 0.023$) in this direction.

It seems likely that there are two different behavioural strategies being used by young baboons with respect to the amount of time spent in close proximity to their mothers. Young infants who are not yet weaned spend more time in contact and close proximity to their mothers although their time spent suckling may be decreased, whereas older infants who are more nutritionally and locomotorally independent spend less time in close proximity to the mother. These data seem to indicate adaptive strategies for coping with a seasonal environment which are differently employed depending on the state of an individual's independence from its mother. An infant who is very dependent on its mother becomes more dependent on her, but an infant who is perhaps semi-independent from its mother, becomes more independent.

Timing of the decline in contact with the mother:

The data on individual differences in time spent in contact with the mother presented in Chapter 5 can be examined with respect to values of food availability. Table 7.2 presents for the five individuals involved (i.e. subjects 6 - 14 months old who exhibited a decline in the amount of time spent in contact with the mother), the ages between which the amount of time spent in contact with the mother declined from $>30\%$ to $<10\%$ of their total time budget, and measures of food availability for the months between which the change occurred. There is a positive correlation between the

Table 7.2: The ages between which five individuals aged from 6 to 14 months old showed a decrease in the amount of time spent in contact with the mother from > 30% to < 10%, and the biomass values for the months between which the change occurred.

ID	AGE (MONTHS)		BIOMASS (g/m ²)	
	> 30%	< 10%	> 30%	< 10%
MC	6	9	0.098	1.546
TP	9	11	0.327	0.617
MO	10	12	1.842	0.327
WG	11	14	1.842	0.098
NP	12	14	1.842	0.327

age at which the amount of time spent in contact was $> 30\%$ and the biomass of food available in that month (Pearson's correlation coefficient, $R = 0.87$, $p = 0.027$). Although the number of subjects is small, these data indicate that there is a pattern in the timing of the decline in time spent in contact with the mother: infants 'weaned' from contact with the mother at an early age did so when food availability was low, whereas those 'weaned' at a later age did so when food availability was higher. One interpretation of this pattern of individual differences in behaviour is that infants are weaned and become independent from their mothers at an early age if environmental conditions are bad, when the cost of having a dependent infant are high for the mother, but if environmental conditions are good, and costs to the mother are lower, they can remain in close contact with her until a later age. For infants that were at younger ages when the decline in contact started, biomass values improved during the months of the from $> 30\%$ to $< 10\%$ time in contact with the mother. However, it seems that this did not promote a return to more time being spent in contact with the mother; rather, once the decline of time spent in contact had started, perhaps as a response to low food availability, it continued its course. Examination of the long-term demographic data from this site in conjunction with the data on food availability over the same period would produce interesting data on the timing of weaning.

In summary, the data presented in this section suggest that there is an interaction between food availability and behaviour associated with the mother-offspring relationship. In months when food is more scarce (the worst months), young infants tend to spend more time in contact with their mothers than in months when food is more abundant (the best months). Infants which are older and young juveniles may adopt a different strategy in months of food scarcity, spending less time in contact with the mother, perhaps as they spend more time foraging independently, rather than becoming more closely associated with her. The timing of weaning for infants aged between 6 and 14 months old may be affected by food availability such that if food availability is low (worst months), infants are weaned at a younger age and therefore,

like the older infants reported here, spend less time in contact with the mother; if food availability is high, infants are weaned later and spend more time in contact with their mother up until this later age.

EFFECTS OF FOOD AVAILABILITY ON BEHAVIOURAL ACTIVITIES

Table 7.3 presents the results of the paired T-tests for the percentage of time spent in the behavioural activities of 'moving', 'environmental exploring', 'social exploring', 'visually attending', 'attending environmental', 'attending social', 'grooming', 'being groomed', 'receiving affiliative approaches', 'initiating affiliative approaches', 'exploring for food' and 'feeding', in the worst and best months.

Moving: There were no significant differences in the amount of time spent moving between the worst and best months for all subjects, or for groups of young infants, older infants and young juveniles. The difference for young juveniles, where less time was spent moving in the worst months than in the best months, approached significance ($df = 4$, $p = 0.080$).

Dunbar (in press) has suggested that baboons increase their rate of travel to prevent their time budgets becoming stressed by an increase in the amount of time spent moving when longer day journeys are necessary to meet the group's daily foraging requirements. In this study, where a negative relationship between day range length and baboon food biomass was found, time spent moving would be conserved by this type of increase in the speed of travelling. These data suggest that juveniles were in fact able to decrease the amount of time they spent moving, thus releasing time to spend in other activities.

Environmentally and socially exploring: There were no significant differences in the amount of time spent environmentally exploring between the worst and best months for all subjects, or for groups of young infants, older infants and young juveniles, although the difference between time spent environmentally exploring in the worst and best months by older infants, where more time was spent in this activity in

Table 7.3: Paired T-tests for the percentage of time spent in behavioural activities in the worst and best months

		Worst	Best	t	df	p
Moving:	ALL SUBJECTS	-1.06	0.72	1.47	17	0.161
	YOUNG INFANTS	-0.020	-1.06	0.44	5	0.681
	OLDER INFANTS	-0.18	0.72	0.81	6	0.447
	JUVENILES	-3.32	2.84	2.34	4	0.080
Environmental Exploring:	ALL SUBJECTS	0.71	-0.33	1.78	17	0.093
	YOUNG INFANTS	1.94	-0.66	1.60	5	0.171
	OLDER INFANTS	0.42	-0.06	2.26	6	0.064
	JUVENILES	-0.34	-0.30	1.09	4	0.337
Social Exploring:	ALL SUBJECTS	-0.63	0.47	2.45	17	0.025*
	YOUNG INFANTS	-0.57	1.22	1.42	5	0.216
	OLDER INFANTS	-1.02	-0.10	3.02	6	0.023*
	JUVENILES	-0.17	0.38	1.03	4	0.359
Visually Attending:	ALL SUBJECTS	-0.58	0.64	1.09	17	0.291
	YOUNG INFANTS	0.49	-0.07	0.21	5	0.839
	OLDER INFANTS	-1.27	0.80	1.32	6	0.236
	JUVENILES	-0.88	1.27	1.52	4	0.203
Attending Environmental:	ALL SUBJECTS	0.20	0.45	2.99	17	0.008**
	YOUNG INFANTS	0.29	0.66	1.49	5	0.196
	OLDER INFANTS	0.18	0.40	4.29	6	0.005**
	JUVENILES	0.11	0.27	1.89	4	0.131
Attending Social:	ALL SUBJECTS	0.15	0.41	4.23	17	0.001***
	YOUNG INFANTS	0.28	0.48	1.87	5	0.121
	OLDER INFANTS	0.11	0.43	3.17	6	0.019*
	JUVENILES	0.07	0.29	1.91	4	0.128

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

Table 7.3 continued.

		Worst	Best	t	df	p
Grooming:	ALL SUBJECTS	-0.70	-0.39	0.49	17	0.630
	YOUNG INFANTS	0.12	-0.11	0.81	5	0.455
	OLDER INFANTS	-0.06	-0.67	0.69	6	0.514
	JUVENILES	-2.58	-0.33	1.27	4	0.274
Being Groomed:	ALL SUBJECTS	1.97	2.42	0.66	17	0.519
	YOUNG INFANTS	3.20	1.50	1.66	5	0.158
	OLDER INFANTS	1.24	2.87	1.67	6	0.146
	JUVENILES	1.51	2.90	1.11	4	0.330
Receiving	ALL SUBJECTS	-0.06	0.03	2.96	17	0.009**
Affiliative	YOUNG INFANTS	-0.05	0.06	1.54	5	0.185
Approaches:	OLDER INFANTS	-0.10	0.02	2.85	6	0.029*
	JUVENILES	-0.04	0.00	0.77	4	0.486
Initiating	ALL SUBJECTS	0.22	0.42	3.41	17	0.003**
Affiliative	YOUNG INFANTS	0.21	0.53	3.13	5	0.026*
Approaches:	OLDER INFANTS	0.19	0.34	3.25	6	0.017*
	JUVENILES	0.27	0.38	0.73	4	0.508
Exploring for Food:	ALL SUBJECTS	0.32	0.16	0.23	17	0.821
	YOUNG INFANTS	-0.87	0.43	2.88	5	0.034*
	OLDER INFANTS	0.10	0.46	0.37	6	0.726
	JUVENILES	2.06	-0.59	1.52	4	0.202
Feeding:	ALL SUBJECTS	3.57	-1.84	3.02	17	0.008**
	YOUNG INFANTS	-0.12	-0.02	0.04	5	0.970
	OLDER INFANTS	4.50	-2.18	2.50	6	0.047*
	JUVENILES	6.70	-3.55	3.25	4	0.031*

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

the worst months, approached significance ($df = 6$, $p = 0.064$).

In contrast, there was a significant difference over all subjects in the amount of time spent socially exploring between the worst and best months, where less time was spent in this activity in the worst months. Young infants and juveniles showed no significant differences in their behaviour, but older infants spent significantly less time socially exploring in the worst months than in the best months.

Lee (1986) reports that for vervet monkeys, seasonal cycles in social play were strongly related to changes in the availability and quality of foods, where time spent playing was less in the dry season when dietary quality was low. Barrett et al. (in press) show that the frequency and quality of play in young geladas are related to habitat quality, where rates of play declined as environmental conditions deteriorated as the dry season progressed and more time was required to be spent feeding. Oliver and Lee (1978) report that the frequency of social play was highest in the wet season for troops of baboons at Gombe and Ruaha, Tanzania. The results presented here for 'socially exploring' are consistent with these findings and can be seen to support the view of Martin and Caro (1985) that play is sensitive to prevailing conditions.

Martin and Caro (1985) suggest that play is unlikely to be crucial for normal development since some species perform this activity (e.g. rats) while other closely related species (e.g. mice) do not, and Lee (1986) comments that seasonal constraints on rates of social play have not been shown to have a major effect on development. However, Barrett et al. (in press) suggest that seasonal effects on social play behaviour may have an impact on the early social experience of juvenile gelada baboons by influencing the availability of play partners and the nature of the interactions. With respect to the activities of environmental and social exploring used in this study, different patterns of developmental change have been demonstrated for these exploring behaviours (Chapter 6) which have been interpreted as indicating that the two behavioural activities are functionally different. The results of time spent in these activities during worst and best months presented in this chapter also indicate a difference between these aspects of behaviour in the effect of periods of food scarcity:

time spent environmentally exploring is at least maintained (there is even a trend towards an increase) in times of food scarcity, whereas the time spent socially exploring is reduced. So distinguishing these aspects of exploring implies that time spent environmentally exploring is functionally more important and is maintained, whereas time spent socially exploring can be lost without cost to the individuals. It is possible that time spent socially exploring can be 'caught up' later when conditions are better, but time spent environmentally exploring during infancy cannot be missed. If it were possible to have longitudinal data on these subjects, it would be very interesting to see how the amount of environmental and social exploring, and therefore experience of the physical and social environment, would correlate with life time survivorship.

In particular, it is older infants that exhibit a difference in the time spent socially exploring. This age group also shows a (non-significant) tendency to change the amount of time spent environmentally exploring between the worst and best months. These data suggest that the time budgets of older infants have to be adjusted between these modes of exploring in order for them to cope with seasonal periods of food scarcity, rather than the proportions of time spent in each activity being maintained across seasonal fluctuations in food availability.

Visually attending: There were no significant differences in the amount of time spent visually exploring between the worst and best months for all subjects, or for groups of young infants, older infants and young juveniles. If this behavioural activity is viewed as being equivalent to that of 'resting' used in other studies (see Chapter 6), these data suggest that in this study time spent resting was maintained when environmental conditions became harsher and did not decrease in response to increases in time spent in other behavioural activities during the worst months as suggested by Dunbar and Sharman (1984).

Attending environmental and attending social: In contrast with the general behavioural category of 'visually attending', time spent attending environmental and attending social both show significant differences in the amount of time spent in these activities. More time was spent environmentally and socially attending in the best

months than in the worst months. This difference in behaviour is possibly because in the best months there may be more events to attend to (e.g. more social interactions; a wider variety of food types being eaten), but there are no objective measures to substantiate this interpretation. In particular, it is again the age group of older infants who show seasonal change in the time spent in these behavioural activities.

Grooming and being groomed: There were no significant differences in the amount of time spent grooming or being groomed between the worst and best months for all subjects, or for groups of young infants, older infants and young juveniles. These data indicate that time spent in these social activities was maintained in periods of food scarcity (in contrast with the time spent socially exploring). Dunbar and Sharman (1984) propose that social time is conserved when time budgets are being stressed. The data presented here are consistent with that view. It would be interesting to examine the identity of the partners that are grooming/being groomed by subjects in the worst and best months. One adaptation to seasonal stress might be to consistently groom fewer individuals or only those which are closely related to the subject, rather than a broader range of individuals.

Receiving and initiating affiliative approaches: A significant seasonal effect, however, was found on the time spent on receiving affiliative approaches and initiating affiliative approaches. Over all subjects, more time was spent receiving affiliative approaches and initiating affiliative approaches in the best months than in the worst months. In both cases, older infants exhibited a significant difference in behaviour ($df = 6$, $p = 0.029$ and 0.017 respectively) and young infants showed a significant difference in the time spent initiating affiliative approaches ($df = 5$, $p = 0.026$), where more time was spent in this activity in the best months. During periods of food scarcity therefore, less time was spent involved in these brief social interactions. It might have been expected that time spent in social interactions of longer duration (i.e. grooming/being groomed) would be 'given up' in the worst months, and that brief greetings and social interactions which have small time costs, would be maintained in activity budgets, possibly even increasing in occurrence. However, the data presented

here do not support this hypothesis.

Exploring for food: There was no significant difference in the time spent exploring for food between the worst and best months over all subjects. Older infants and young juveniles showed no significant difference in the time spent in this activity, but young infants spent significantly less time exploring for food in the worst months than in the best months ($df = 5$, $p = 0.034$). Older infants and young juveniles therefore seemed to maintain the amount of time spent exploring for food at times of food scarcity. The significant difference in the behaviour of young infants can be interpreted as indicating that at times of food scarcity, instead of looking for solid food items to eat, young infants can rely on their mothers for nutritional intake and do not spend time exploring for food; however, the data presented earlier on the time spent at the nipple (an indication of intake of milk) show no significant difference between the best and worst periods.

Feeding: There was a significant difference over all subjects in the amount of time spent feeding between the worst and best months, where more time was spent in this behavioural activity in the worst months than in the best months. In particular, older infants and young juveniles showed this significant change in behaviour between the worst and best months ($df = 6, 4$; $p = 0.047$ and 0.031 respectively), whereas young infants showed no significant change in behaviour. Young infants showed no difference in time spent feeding on solid foods, perhaps because at that age they were still relying on their mothers milk, rather than solid foods, for nutrition.

Altmann (1980) reports that adult females spent less time feeding after the rainy period. Oliver and Lee (1978), however, found a difference between the pattern of seasonal feeding at two different sites: at Gombe, less time was spent feeding by juveniles in the wet season, but at Ruaha when food became more abundant in the wet season, time spent feeding by juveniles increased. These differences in behaviour indicate that there is a complex of environmental factors effecting time spent feeding.

There are therefore reasons to expect time spent feeding to increase in times of food abundance or in times of food scarcity, and the data presented here support the

latter hypothesis for conditions at Cholulu. This finding is investigated further in the next section, where the foods eaten by each age group during the worst and best months are examined.

In summary, significantly less time was spent socially exploring, environmentally and socially attending and receiving and initiating affiliative approaches in the worst months; significantly more time was spent feeding in the worst months. In most cases, older infants were the age group which exhibited these differences in behaviour. Time spent in other behavioural activities seemed to be maintained across the worst and best months. For young baboons therefore, some behavioural activities show no significant differences in the amount of time spent in the activity between worst and best months, indicating that those parts of the time budget are maintained during periods of food scarcity, perhaps even preserved; other parts of the time budget are stressed in times of food scarcity, and a change in the proportion of time spent in those activities is effected so that sufficient nutrients can be obtained during the active day. The nature of the foods being eaten will affect parts of time budgets (for example, the amount of time spent feeding, exploring for food, moving). The foods being eaten in the worst and best months is examined in the next section. Flexibility in the allocation of time budgets can be seen as an adaptive strategy for coping with living in a seasonal environment, as mentioned in Chapter 1.

VARIATION IN THE DIET OF YOUNG BABOONS

The top ten foods eaten each month by each age group and for a group of mothers are listed in Appendix F. The diets of young infants, older infants and young juveniles were examined for seasonal variation by calculating the mean percentage of total feeding time spent on each different food type eaten in the worst and best months. Figures 7.8(a) - (c) present an analysis of the foods which accounted for two-thirds (66.1 - 67.4%) of the total time spent feeding separately for each group. The

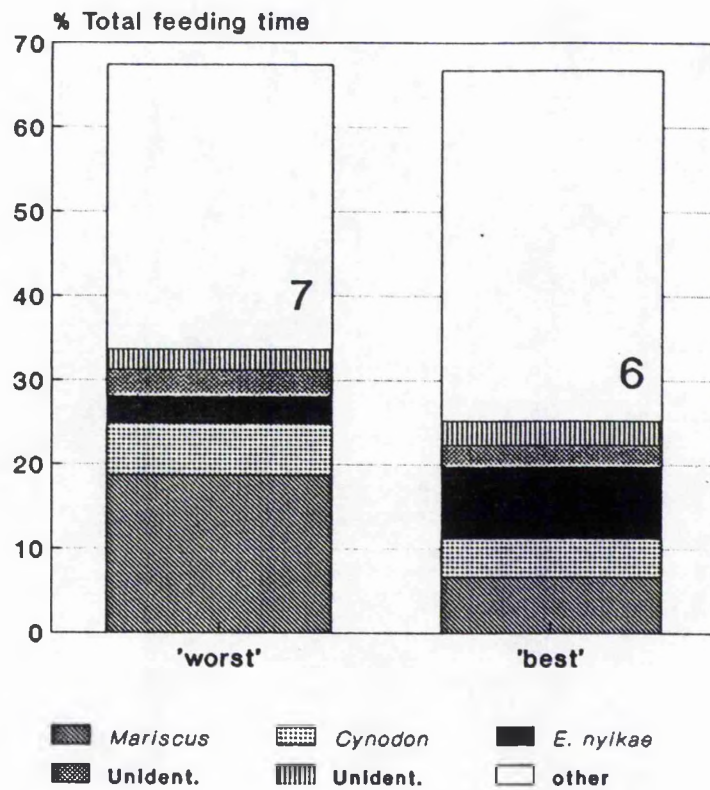


Figure 7.8(a): The proportion of total feeding time spent eating seasonally shared foods by young infants, when the foods which accounted for two-thirds of the total time spent feeding were examined. The number of other food types which account for the remaining amount of time is also presented for 'worst' and 'best' months.

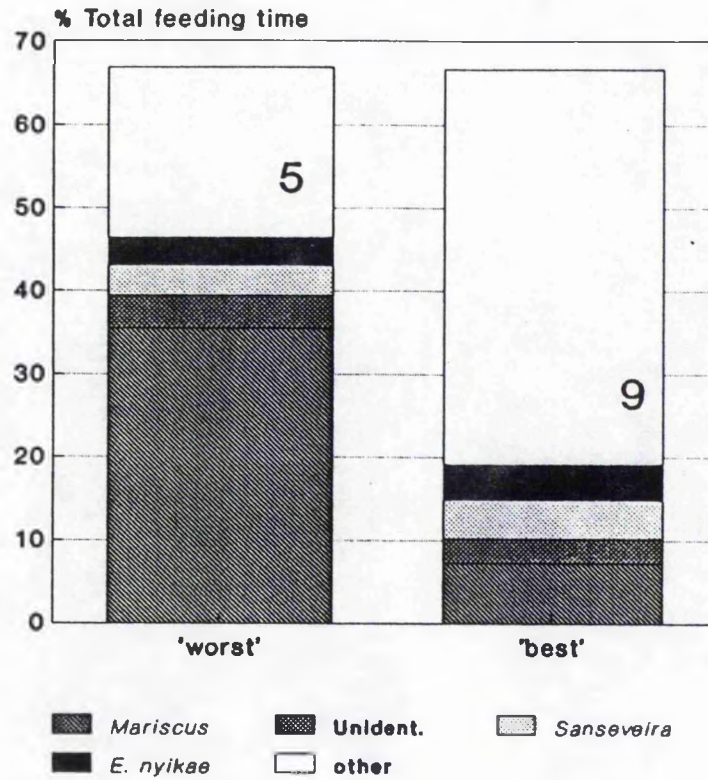


Figure 7.8(b): The proportion of total feeding time spent eating seasonally shared foods by older infants, when the foods which accounted for two-thirds of the total time spent feeding were examined. The number of other food types which account for the remaining amount of time is also presented for 'worst' and 'best' months.

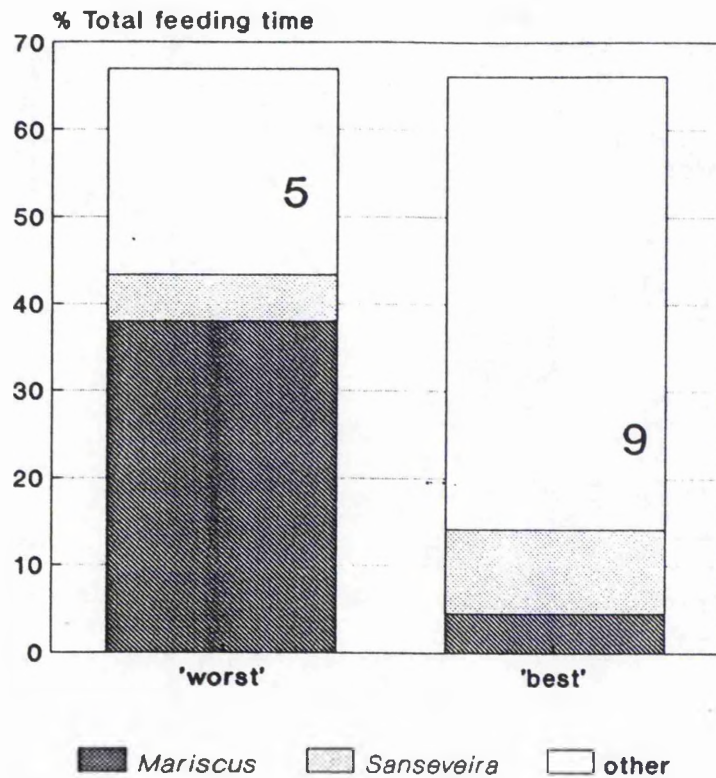


Figure 7.8(c): The proportion of total feeding time spent eating seasonally shared foods by young juveniles, when the foods which accounted for two-thirds of the total time spent feeding were examined. The number of other food types which account for the remaining amount of time is also presented for 'worst' and 'best' months.

percentage of total feeding time spent on foods eaten in both the worst and best months is presented, together with the number of food types which accounted for the remaining proportion of the feeding time. A list of these seasonally shared and seasonally unique food types and the percentage of time spent feeding on each of these food types is presented in Table 7.4, separately for each age group.

For two-thirds of the total feeding time, young infants ate five food types in common between the worst and best months, and in the worst and best months fed on seven and six different food types respectively (Figure 7.8(a)). Older infants ate four food types in common, and fed on five and nine different food types in the worst and best months respectively (Figure 7.8(b)). Young juveniles fed on two food types in common between the worst and best months, and ate five and nine different food types in these two periods (Figure 7.8(c)).

These data suggest that during months of lower food availability, older infants and young juveniles fed on a *less diverse* diet than during times of higher food availability. This is consistent with the finding of Post (1981) for adult baboons at Amboseli (see Chapter 1: Seasonality). Examination of the diversity of diet in the context of the number of food types available in these periods would also be interesting.

The data presented in the previous section indicate that more time is spent feeding in the worst months than in the best months, so it is likely these fewer food types eaten in the worst months take more time to ingest than the greater diversity of food types eaten in the best months. The list of food types in Table 7.4 are consistent with this suggestion; for example, *Mariscus amauiropus* bases which are eaten for a high proportion of time in the worst months are very likely to be harder to ingest than *Acacia* spp. flowers which are eaten for a high proportion of the time in the best times.

Data on dietary variation and time spent feeding need to be analysed in the context of detailed data on food availability, beyond the simple distinction made here between worst and best months i.e. monthly variation should be examined with respect to the nature of the foods available (the ease with which they can be obtained and their nutritional content). An analysis of rates of nutrient intake is necessary to properly

Table 7.4: Baboon foods eaten in the 'worst' and 'best' months by young infants, older infants and young juveniles, and the mean percentage of total feeding time spent on each food type, listed in order of time spent feeding. Foods eaten in both the 'worst' and 'best' months are underlined.

W O R S T		B E S T	
SPECIES/PART	% TIME	SPECIES/PART	% TIME
YOUNG INFANTS			
<u>Mariscus amauiropus/bases</u>	18.7	<u>Acacia etbaica/flowers</u>	14.6
<u>Mariscus amauiropus/scraps</u>	15.1	<u>Acacia tortilis/flowers</u>	10.7
<u>Acacia nilotica/seeds</u>		<u>Euphorbia nyikae/scraps</u>	8.7
(fresh pods)	7.5	<u>Acacia etbaica/exudate</u>	8.5
<u>Cynodon spp/blades</u>	6.1	<u>Mariscus amauiropus/bases</u>	6.7
<u>Euphorbia nyikae/scraps</u>	3.3	<u>Cynodon spp/blades</u>	4.5
<u>Unidentifiable brown thing</u>	3.1	<u>Unidentifiable thing</u>	2.9
<u>Acacia nilotica/seeds</u>		<u>Lyceum europeum/leaves</u>	2.7
(dry pods)	2.4	<u>Acacia etbaica/dry seed</u>	2.7
<u>Opuntia vulgaris/pads</u>	2.4	<u>Unidentifiable brown thing</u>	2.5
<u>Unidentifiable thing</u>	2.4	<u>Penissitum spp/blades</u>	2.3
<u>Ipomea mombassana/flowers</u>	2.3		
<u>Acacia etbaica/seeds</u>			
(dry pods)	2.1		
<u>Acacia nilotica/scraps</u>	1.8		
12 food types		11 food types	
OLDER INFANTS			
<u>Mariscus amauiropus/bases</u>	35.5	<u>Cynodon spp/blades</u>	11.5
<u>Acacia nilotica/seeds</u>		<u>Acacia tortilis/flowers</u>	8.4
(fresh pods)	4.3	<u>Acacia etbaica/flowers</u>	7.3
<u>Unidentifiable brown thing</u>	3.9	<u>Mariscus amauiropus/bases</u>	7.3
<u>Mariscus amauiropus/scraps</u>	3.6	<u>Acacia etbaica/exudate</u>	6.2
<u>Sanseveira intermedia/bases</u>	3.6	<u>Sanseveira intermedia/bases</u>	4.7
<u>Euphorbia nyikae/scraps</u>	3.5	<u>Euphorbia heterachroma/stems</u>	4.5
'large' <u>Ipomea spp/flowers</u>	3.1	<u>Euphorbia nyikae/scraps</u>	4.4
<u>Acacia nilotica/seeds</u>		<u>Unidentifiable brown thing</u>	2.9
(dry pods)	2.5	<u>Acacia etbaica/dry seed</u>	2.7
<u>Unidentifiable thing</u>	2.5	<u>Lyceum europeum/leaves</u>	2.3
		<u>Euphorbia nyikae/pads</u>	2.3
		<u>Grewia tembensis/fruits</u>	2.2
9 food types		13 food types	
YOUNG JUVENILES			
<u>Mariscus amauiropus/bases</u>	38.0	<u>Acacia tortilis/flowers</u>	9.9
<u>Acacia nilotica/seeds</u>		<u>Acacia etbaica/flowers</u>	9.6
(fresh pods)	8.2	<u>Sanseveira intermedia/bases</u>	9.6
<u>Acacia etbaica/seeds</u>		<u>Lyceum europeum/leaves</u>	6.8
(fresh pods)	5.4	<u>Acacia etbaica/exudate</u>	6.5
<u>Sanseveira intermedia/bases</u>	5.4	<u>Cynodon spp/blades</u>	5.7
<u>Euphorbia nyikae/pads</u>	3.7	<u>Mariscus amauiropus/bases</u>	4.5
<u>Acacia nilotica/seeds</u>		<u>Euphorbia heterachroma/stems</u>	3.8
(dry pods)	3.4	<u>Penissitum spp/blades</u>	3.6
<u>Unidentifiable thing</u>	2.4	<u>Grewia tembensis/fruits</u>	3.1
		<u>Acacia etbaica/dry seed</u>	3.0
7 food types		11 food types	

elucidate the relationship between time spent feeding and variation in diet.

CONCLUDING DISCUSSION

Fitting developmental curves to behavioural data and analysing residual values has been developed to elucidate environmental effects on intra-specific variation. During the development of this technique, a detailed investigation of the appropriate shapes of curve to model the developmental change in various behavioural activities was carried out as suggested by Rasmussen and Tan (in press). The resulting set of curves should provide a useful model for any further investigation of developmental change. This technique of examining residuals could equally be used to hold the effects of seasonality constant as a baseline, to examine the variation due to development.

These data show that behaviour is affected by the availability of food. The periods of 'worst' and 'best' months used in this study actually represent periods of 'less abundant' and 'more abundant' food. In fact, for months outside the period of focal data collection, there were higher values of baboon food biomass than for the best months used in these analyses (see Figure 3.16), and the long-term records show that at this site there have also been periods of drought and very scarce food resources. Greater differences in behaviour might be expected if data from more extreme periods were compared.

In his recent paper which showed that the diet of yearling females can predict their life time fitness, S. Altmann (1991) demonstrates that the behaviour of young baboons has important implications for their future. The research reported in this thesis has described the behaviour of young baboons in more comprehensive detail than has been previously published, against which data from other sites has been compared and can be compared in the future. However, Altmann deals only with the nutrient and energy intakes of these individuals and does not consider the relationship between environmental conditions (food availability) and individuals' behaviour. Such factors, which influence nutrient intake, are ignored. The aim of this thesis was to examine the

impact of one of these factors, namely seasonality, on the behaviour of young baboons who were thought to be a particularly vulnerable age group. I now conclude by discussing these aspects of behavioural ecology.

What effects do seasonal fluctuations in food availability have on young baboons?:

The data presented in this thesis show that in months where food was more scarce, young baboons spent more time feeding, and less time in various socially related and attentional behavioural activities. The time spent in other behaviours was maintained across periods of scarcer food. Different diets were eaten in times of food scarcity and in times of more abundant food. There is also some indication that the scheduling and nature of the weaning process, and therefore of development, was influenced by food availability.

Seasonal changes in activity budget, where there is an increase in time spent in one activity and a corresponding decrease in other activities in relation to food availability (such as those discussed in this chapter), are non-fatal effects of seasonality. This behavioural flexibility can be seen as an adaptation which enables these young baboons to survive in a fluctuating environment. However, time budgets have limitations, so if more time is required for an individual to perform essential activities such as feeding than is available, then when activities such as exploring for food and moving are affected, this may result in the death of that individual.

Are individuals in this age group particularly vulnerable to the effects of seasonal stress?

The data presented here suggest that one subgroup of the young baboons studied, namely older infants (weanlings), could be particularly vulnerable to the effects of seasonality.

From these data, it seems likely that young infants responded to seasonal fluctuations in food availability by spending more time in close proximity to their mothers, less time exploring for food and no significant difference in time spent feeding

in periods of scarcer food. This implies that at this age, young baboons are buffered against the effects of seasonal stress by their mothers' behaviour as suggested in Chapter 1, and so did not experience many costs during times of food scarcity (although there may be costs to the mother). Young juveniles did not exhibit significant behavioural changes in their activity budgets apart from spending more time feeding in periods of food scarcity, so although more time had to be devoted to feeding, there were no clear costs to their behavioural budget. However, older infants showed several changes in their activity budgets in response to lower food availability, such that more time was spent feeding and less time was spent in some other activities. These semi-independent individuals clearly have to significantly adjust their time budgets to cope with food scarcity. With limitations on how much adjustment can be made within a time budget before balancing the budget becomes impossible, older infants are therefore probably under more stress from seasonal fluctuations in the environment and are therefore more vulnerable to the effects of extreme seasonal stress than other age groups at this site.

Further analyses and future research:

Further analyses of the data from this study site should involve examining in more detail the feeding behaviour of these young baboons, for example, their bite rates and nutritional intake, on a monthly basis. These data can then be analysed in the context of food availability on a more specific monthly basis than that used in this thesis, in order to explain variation in behaviour. The long-term demographic records from this site should be examined in conjunction with the long-term records on ecology with respect to seasonal fluctuations in food availability, in order to explain life history patterns.

Further research into the effects of environmental factors could involve studies on this age group of primates at sites which vary in habitat quality and in their degree of seasonality. A comparative study of weanling baboons in an environment which does not experience such seasonal stresses would be instructive. In a seasonal

environment, future studies should ensure that data are collected over a longer period of time than was possible in this study, so that more than one seasonal change in food availability is experienced. Ecological data should perhaps be collected on a more frequent basis, to provide more comprehensive information on environmental fluctuations. In particular, it would be interesting to investigate the relationship between infants' acquisition of independence (i.e. the start and duration of the period of vulnerability) and food availability, for example, the availability and use of 'weaning' foods. Other factors such as temperature, substrate features and water resources in the physical environment, and support from the social environment (e.g. adult males), should also be incorporated into analyses of the behaviour of young baboons.



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APPENDIX A

DEFINITIONS OF BEHAVIOURAL CATEGORIES

(i) ACTIVITY BUDGET CATEGORIES (subdivision 1):

FEEDING: ingestion of food items. A feeding bout is started when the food item is passed from hand to mouth or is harvested directly by the mouth, and ended when chewing appears to have finished or the animal has moved five body lengths from the food. Food codes include ones for milk, water, previously picked food items, food from cheek pouches and unidentifiable foods.

SUPPLANTING: another individual moves to avoid the focal subject who then accesses a food item at that site.

BEING SUPPLANTED: avoiding another individual at a feeding site and losing access to a food item there.

SUFFERING REJECTION: receiving a physical movement by mother to direct the subject away from her, and the associated subject response (moaning, screaming). This includes being struck and/or a weaning tantrum, and this characteristic moaning and screaming behaviour even when it is not discernably promoted by the mother's immediate actions.

INITIATING AFFILIATIVE APPROACH: making a brief affiliative interaction i.e. greeting, lipsmacking, presenting, mounting.

RECEIVING AFFILIATIVE APPROACH: being the receiver of a brief affiliative interaction as defined above and being receptive to it.

AVOIDING: moving unaffected away from another individual in fear; moving and hiding from another individual.

INITIATING AGGRESSION: threatening another individual i.e. lunging, pushing, hitting, eyelid flashes, vocalisations.

RECEIVING AGGRESSION: being the receiver of aggression or a threat as defined above; provoked scream or fear grimace by another individual.

CARRIED BY MALE: subject transported by an adult or subadult male individual dorsally or ventrally or otherwise when there is no conflict present.

WITH MALE IN CONFLICT: subject associated with an adult or subadult male during an aggressive conflict.

IN NIPPLE POSITION: on ventrum or similar position where the subject has the potential to be on the nipple but it is not clear to the observer whether the nipple is in fact in the subject's mouth.

ON NIPPLE: subject has the nipple in mouth but sucking cannot be seen. (If sucking is observed, then the behaviour is coded as 'feeding' with the food code for milk.)

GROOMING: active removal of parasites, dirt and pieces of skin etc. from the body of another.

BEING GROOMED: grooming performed on the subject by another.

VISUALLY ATTENDING (INDISTINCT): subject sitting or immobile and looking somewhere though the focus point is not clear; also autogrooming. (compare with RESTING)

ATTENDING SOCIAL: a specific subcategory of **VISUALLY ATTENDING** (see above) where the focus of attention is clearly a social interaction e.g. standing on hind legs to watch an aggressive interaction having had attention attracted by screaming; passively observing social behaviour amongst others without interacting self.

ATTENDING ENVIRONMENTAL: a specific subcategory of **VISUALLY ATTENDING** (see above) where the focus of attention is clearly an environmental (i.e. non-social) feature e.g. food that the mother or other is feeding on; predators; local people (potential predators within the environment in which the animal lives).

EXPLORING FOR FOOD: moving through food patch searching for food items, including digging.

ENVIRONMENTAL EXPLORING: manipulation of any physical (i.e. non-social) object including potential food items without a serious prospect of ingestion; clambering around the physical environment (e.g. over *Sansevieria*, in trees) but not as part of the general/group progression (see **MOVING**); solitary play (including chasing insects in play). i.e. active physical interaction with the environment.

SOCIAL EXPLORING: play, rough-and-tumble chasing; interaction with any other individual which is of longer duration than the social interactions defined in **INITIATING AFFILIATIVE APPROACH** and **INITIATING AGGRESSION**. i.e. active social interaction.

ACTIVE EXPLORING: simultaneous occurrence of **ENVIRONMENTAL** and **SOCIAL EXPLORING** so that the subject is exploring an environmental feature with another individual. e.g. two infants focussed on the same object in play, but not clambering in parallel.

MOVING: locomoting when not one of the above behavioural categories (e.g. **ENVIRONMENTAL EXPLORING**, **AVOIDING**).

N.B. this category need not be mutually exclusive of **VISUALLY ATTENDING**.

RESTING: subject inactive and not **VISUALLY ATTENDING**; head down on mother's back when riding dorsally; sunning; sleeping.

OUT OF SIGHT: subject not visible to observer.

(ii) MALE PROXIMITY CATEGORIES (subdivision 2):

WITHIN 1m: subject is in the sustained presence of an adult or subadult male, within 1m of him (including contact). i.e. not just passing within this distance.

1m TO 5m: as above, but the male is between 1m and 5m away. If either the subject or the male is in a tree without the other, then distance is estimated as travelling distance rather than spatial distance.

MORE THAN 5m: there is no adult or subadult male within 5m of the subject.

(iii) MOTHER CONTACT CATEGORIES (subdivision 3):

VENTRAL CONTACT: subject is in contact with its mother's ventrum, sitting or being carried.

OTHER CONTACT: subject is in contact with its mother in any other position than ventrally e.g. dorsally, while grooming, on nipple but not in ventral contact.

WITHIN ARMS' REACH: subject is within arms' reach of its mother.

ARMS REACH TO 5m: subject out of arms' reach of its mother but within 5m of her.

BEYOND 5M: subject is further than 5m away from its mother.

APPENDIX B

'MBUNI':COMPUTER PROGRAM TO RECORD FOCAL ANIMAL BEHAVIOUR

'Mbuni' is composed of two separate programs: MBUNI (the main program) and MB_LIBRARY (to create the library that is used by the main program). It has been structured so that specific functions are dealt with by separately compiled units, as follows:

MBUNI	{main program}
MBUN_TYP	{type definitions}
MBUN_GEN	{basic procedures common to all sections}
MBUN_LIB	{procedures that involve the library}
MBUN_OBS	{procedures involved in making observations}
MBUN_LOC	{procedures involved in recording locations and calculating distance}
MB_LIBRARY	{to create the library}
MBUN_TYP	
MBUN_GEN	

This appendix contains a complete program listing, and the algorithm used in unit MBUN_LOC for calculating distances from 6-figure grid references.

```

{*****}

PROGRAM mbuni;
{=====}

{ A program to record behaviour continuously or by time sampling via direct
observation of focal animals.}

USES Dos,DIP_Crt,
      Mbun_typ, Mbun_gen, Mbun_lib, Mbun_obs, Mbun_loc ;

VAR
  junk: char;

{-----}

PROCEDURE mainmenu;
{ ----- }

  var
    library: librarytype;
    choice: char;

  begin
    initializelibrary(library);
    REPEAT
      ClrScr;
      displayln('MAIN MENU',15,0);
      displayln('Select which option is required ...',3,1);
      displayln('(1) Library',8,2);
      displayln('(2) Observation',8,3);
      displayln('(3) Location',8,4);
      displayln('(4) Quit',8,5);
      displayln('CHOICE',12,6);
      getandcheckentry(20,6,choice,'1','4',1,7);
      CASE choice OF
        '1': librarymenu(library);
        '2': observation(library);
        '3': location
      END
    UNTIL choice = '4'
  end; {mainmenu}

{-----}

BEGIN {main program}
  ClrScr;
  displayln('PROGRAM TO RECORD FOCAL ANIMAL BEHAVIOUR',0,3);
  displayln(' Press any key to continue ... ',1,6);
  waitandgetchar(35,6,junk);
  mainmenu;
  ClrScr;
  displayln(' *** END OF PROGRAM ***',1,3)
END. {main program}

{*****}

```

```
{*****}
```

```
UNIT Mbun_typ;  
{ ===== }
```

```
INTERFACE
```

```
CONST
```

```
maxentries = 70;  
blankline = ' ';  
countkey = 'f';  
RETURN = 13;  
BELL = 7;  
BACKSPACE = 8;  
ESC = 27;  
NUL = 93;  
maxdescription = 18;  
maxpromptinfo = 15;  
maxpromptedinfo = 6;  
libfilename = 'A:library.txt';  
locfilename = 'A:loc_info.txt';  
firstentry = ',';  
lastentry = 'z';  
defaultsubd = '1';  
defaultextrasubd = '0';
```

```
lengthofobsession = 1800;  
CTRLS = 19;  
CTRLE = 5;  
CTRLP = 16;
```

```
errorid = '***';
```

```
TYPE
```

```
timetype = RECORD  
    hours,mins,secs:word  
END;
```

```
datetype = RECORD  
    day,month,year:word  
END;
```

```
messagetype = string[40];
```

```
idtype = string[3];
```

```
entryidtype = ','..'z';
```

```
subdivisiontype = '1'..'4';  
limitedsubdtype = '1'..'3';  
extrasubdtype = '0'..'4';
```

```
modeofrecordingtype = (timesampling,continuous);
```

```
lentrytype = RECORD  
    key: char;  
    description: string[18];  
    subdivision: subdivisiontype;  
    CASE prompt: Boolean OF  
        TRUE: (promptinfo: string[15]);  
        FALSE: ( )  
    END;
```

```

subddetailstype = RECORD
    sd: char;
    extrasubd: extrasubdtype;
    CASE modeofrecording: modeofrecordingtype OF
        timesampling: (lengthoftime:integer);
        continuous: ( )
    END;

```

```

obsdetailstype = ARRAY [limitedsubdtype] OF subddetailstype;

```

```

librarytype = RECORD
    entries: ARRAY [entryidtype] OF lentrytype;
    nrofentries: integer;
    obsdetails: obsdetailstype
END;

```

```

observationtype = RECORD
    k,extrak: char;
    promptedinfo,extrapromptedinfo:string[6];
    time:timetype;
    nrofbites:integer
END;

```

```

obstype = ARRAY [limitedsubdtype] OF observationtype;

```

```

bleepstype = ARRAY [limitedsubdtype] OF timetype;

```

IMPLEMENTATION

END.

{*****}

```

(*****)

UNIT Mbun_gen;
( ===== )

INTERFACE

USES Mbun_typ;

PROCEDURE displayln (mess: messagetype; x,y: byte);
PROCEDURE waitandgetchar (x,y: byte; var cha: char);
PROCEDURE getandcheckentry (x,y:byte; var inp:char; lwb,upb:char;
                           a,b:byte);
PROCEDURE getafterRETURNandcheckentry (x,y:byte; var inp:char;
                                       lwb,upb:char; a,b:byte);
PROCEDURE waitforyorn (x,y:byte; var inp:char);
PROCEDURE enterpositivenumber (x,y:byte; var int:longint; nrofdigits:byte);
FUNCTION fileexists (filename:string): Boolean;

IMPLEMENTATION

USES DIP_Crt,Dos;

PROCEDURE displayln (mess: messagetype; x,y: byte);
( ----- )

begin
  GotoXY(x,y);
  writeln(output, mess) ;
end;

(-----)

PROCEDURE waitandgetchar (x,y: byte; var cha: char);
( ----- )

begin
  GotoXY(x,y);
  write('?':1);
  cha:=ReadKey ;
  GotoXY(x,y);
  write(cha:1)
end;

(-----)

PROCEDURE getandcheckentry (x,y:byte; var inp:char; lwb,upb:char;
                           a,b:byte);
( ----- )

begin
  REPEAT
    waitandgetchar(x,y,inp);
    if (NOT (inp in [lwb..upb])) OR (inp in ['[','\''']) OR (inp = '-')
      OR (inp = '=') OR (inp = '@')
    then displayln('Incorrect entry - enter an alternative',a,b)
  UNTIL (inp in [lwb..upb]) AND (NOT (inp in ['[','\'''])) AND (inp<>'-' )
    AND (inp<>'=') AND (inp<>'@');
  displayln(blankline,a,b)
end;

(-----)

```

```

PROCEDURE getafterRETURNandcheckentry (x,y:byte; var inp:char;
{ ----- }   lwb,upb:char; a,b:byte);

var cha:char;

begin
  inp:=chr(RETURN);
  REPEAT
    REPEAT
      GotoXY(x,y);
      cha:=ReadKey;
      if cha <> chr(RETURN)
      then begin
        inp:=cha;
        if inp = chr(BACKSPACE)
        then write(' ':1)
        else write(inp:1)
        end
      UNTIL cha = chr(RETURN);
      if (inp = chr(RETURN)) OR (inp = chr(BACKSPACE))
      then displayln('Make a key entry!',a,b)
      else if (NOT (inp in [lwb..upb])) OR (inp in [' '..'''])
        OR (inp = '-') OR (inp = '=') OR (inp = '@')
        then displayln('Incorrect entry - enter an alternative',a,b)
      UNTIL (inp in [lwb..upb]) AND (NOT (inp in [' '..'''])) AND (inp<>'-' )
        AND (inp<>'=' ) AND (inp<>'@');
      displayln(blankline,a,b)
    end; {getafterRETURNandcheckentry}

{-----}

PROCEDURE waitforyorn (x,y:byte; var inp:char);
{ ----- }

begin
  REPEAT
    waitandgetchar(x,y,inp)
    UNTIL (inp = 'Y') OR (inp = 'y') OR (inp = 'N') OR (inp = 'n')
  end;

{-----}

PROCEDURE enterpositivenumber (x,y: byte; var int:longint;
{ ----- }   nrofdigits:byte);

var
  cha,inp:char;
  i:byte;

begin
  i:=x;
  int:=0;
  REPEAT
    REPEAT
      GotoXY(i,y);
      cha:=Readkey;
      if cha <> chr(RETURN)
      then begin
        inp:=cha;
        if inp = chr(BACKSPACE)

```

```

        then begin
            if i > x
            then begin
                GotoXY(i-1,y);
                write(' ':1);
                int:=(int DIV 10);
                i:=i-1
            end
        end
    else begin
        write(inp:1);
        if NOT (inp in ['0'..'9'])
        then begin
            displayln('Incorrect entry - enter a digit',
                    1,7);

            Delay(2000);
            GotoXY(i,y);
            write(' ':1);
            GotoXY(i,y)
        end
        else begin
            int:=(int*10) + (ord(inp)-48);
            i:=i+1;
            if ((i-x) > nrofdigits)
            then begin
                displayln
                    ('Too many digits - enter another no.',
                    1,7);

                displayln(blankline,1,y);
                int:=0;
                i:=x
            end
        end
    end;
    displayln(blankline,1,7)
end
UNTIL cha = chr(RETURN);
if i = x
then displayln('Make an entry!',1,8);
Delay(1000);
displayln(blankline,1,8)
UNTIL i > x
end; {enterpositivenumber}

{-----}

FUNCTION fileexists (filename:string): Boolean;
{ ----- }

var textfile:text;

begin
    assign(textfile,filename);
    {$I-}
    reset(textfile);
    {$I+}
    fileexists:= IOResult = 0
end;

END.

{*****}

```



```

{*****}

UNIT Mbun_lib;
{ ===== }

INTERFACE

USES Mbun_typ;

PROCEDURE initializelibrary (var library:librarytype);
PROCEDURE librarymenu (var library: librarytype);
FUNCTION nrofsubdivisions (library:librarytype): integer;

IMPLEMENTATION

USES DIP_Crt,Dos,Mbun_gen;

PROCEDURE initializelibrary (var library:librarytype);
{ ----- }

    var i:char;

    begin
        FOR i:= firstentry TO lastentry DO
            library.entries[i].key:='*';
            library.nrofentries:=0;
            FOR i:= '1' TO '3' DO
                library.obsdetails[i].sd:='*'
            end;
        end;

    {-----}

    FUNCTION nrofsubdivisions (library:librarytype): integer;
    { ----- }

        var count: integer;
            i: char;

        begin
            count:=0;
            FOR i:='1' TO '3' DO
                if library.obsdetails[i].sd <> '*'
                then count:=count+1;
            end;
            nrofsubdivisions:=count
        end;

    {-----}

    PROCEDURE displayoneentry (entry: lentrytype; y:byte);
    { ----- }

        begin
            WITH entry DO
                begin
                    displayln(key,1,y);
                    displayln(description,3,y);
                    displayln(subdivision,22,y);
                    if prompt
                    then displayln(promptinfo,26,y)
                end
            end;
        end; ( displayoneentry)

```

{-----}

```
PROCEDURE displayentries (library:librarytype);
{ ----- }

    const
        starty = 1;
        maxy = 6;

    var
        y: byte;
        i,junk: char;

    begin
        clrscr;
        displayln('K Description      S/d  Prompt      ',1,0);
        y:=starty;
        FOR i:=firstentry TO lastentry DO
            begin
                if (library.entries[i].key <> '**') AND (y <> maxy)
                then begin
                    displayoneentry(library.entries[i],y);
                    y:=y+1;
                end;
                if y = maxy
                then begin
                    displayln('Press any key to continue ...',1,7);
                    waitandgetchar(31,7,junk);
                    clrscr;
                    displayln
                        ('K Description      S/d  Prompt      ',1,0);
                    y:=starty;
                end;
            end;
        displayln('End of library',12,y);
        displayln('Press any key to continue ...',1,7);
        waitandgetchar(31,7,junk);
    end; {displayentries}
```

{-----}

```
PROCEDURE displaysubddetails (library:librarytype);
{ ----- }

    const starty = 1;

    var
        i:char;
        y:byte;

    begin
        clrscr;
        displayln('S/d Extra s/d Mode of rec. Length of tm.',0,0);
        y:=starty;
        FOR i:='1' TO '3' DO
            WITH library.obsdetails[i] DO
                if sd <> '**'
                then begin
                    displayln(sd,1,y);
                    displayln(extrasubd,5,y);
                end;
            end;
        end;
    end;
```

```

        if modeofrecording = continuous
        then displayln('continuous',14,y)
        else begin
            displayln('timesample',14,y);
            GotoXY(27,y);
            writeln(lengthoftime:5)
        end;
        y:=y+1
    end;
    displayln('Press any key to continue ...',1,5);
    waitandgetchar(31,5,i)
end; {displaysubddetails}

{-----}

PROCEDURE display (library:librarytype);
{ ----- }

    var choice:char;

begin
    clrscr;
    if library.nrofentries = 0
    then begin
        displayln('There are no entries in the library',3,3);
        Delay(3000)
    end
    else REPEAT
        clrscr;
        displayln('DISPLAY MENU',12,1);
        displayln('(1) Display library entries',4,2);
        displayln('(2) Display details about the',4,3);
        displayln('subdivisions used during observation',2,4);
        displayln('(0) Quit and return to library menu',4,5);
        displayln('CHOICE ...',12,6);
        getandcheckentry(24,6,choice,'0','2',1,7);
        CASE choice OF
            '1': displayentries(library);
            '2': displaysubddetails(library)
        END
    UNTIL choice = '0'
end; {display}

{-----}

PROCEDURE load (var library:librarytype);
{ ----- }

    var
        textfile:text;
        inp:char;
        tempentry:lentrytype;
        i:byte;
        tempsubddetails:subddetailstype;
        recordingmode:char;

begin
    clrscr;
    inp='!';
    assign(textfile,libfilename);

```

```

if library.nrofentries <> 0
then begin
    displayln('The current library in memory',1,2);
    displayln('will be overwritten',1,3);
    displayln('CONTINUE ... ? Y/N',5,5);
    waitforyorn(30,5,inp);
    if (inp = 'Y') OR (inp = 'y')
    then initializelibrary(library);
    clrscr
end;
if (inp <> 'N') AND (inp <> 'n')
then if NOT (fileexists(libfilename))
then displayln('There is no library on disk',3,6)
else begin
    displayln('Loading begins ...',4,1);
    reset(textfile);
    read(textfile,inp);
    while (inp <> '#') AND (library.nrofentries< maxentries) DO
    begin
        tempentry.key:=inp;
        read(textfile,inp,inp);
        tempentry.description:='';
        i:=1;
        while inp <> ' ' DO
        begin
            tempentry.description:=tempentry.description+inp;
            read(textfile,inp);
            i:=i+1
        end;
        while i <= (maxdescription +1) DO
        begin
            read(textfile,inp);
            i:=i+1
        end;
        tempentry.subdivision:=inp;
        if eoln(textfile)
        then begin
            tempentry.prompt:=FALSE;
            readln(textfile)
        end
        else begin
            tempentry.prompt:=TRUE;
            readln(textfile,inp,tempentry.promptinfo)
        end;
        library.entries[tempentry.key]:=tempentry;
        library.nrofentries:=library.nrofentries +1;
        read(textfile,inp)
    end;
    if (library.nrofentries = maxentries) AND (inp <> '#')
    then REPEAT
        readln(textfile,inp)
        UNTIL inp = '#';
    readln(textfile);
    while (NOT eof(textfile)) DO
    begin
        read(textfile,tempsubddetails.sd,inp,
            tempsubddetails.extrasubd,inp,recordingmode);
        CASE recordingmode OF
            'c': begin
                tempsubddetails.modeofrecording:=continuous;
                readln(textfile)
            end;

```

```

        't': begin
            tempsubddetails.modeofrecording:=timesampling;
            REPEAT
                read(textfile,inp)
            UNTIL inp = ' ';
            readln(textfile,tempsubddetails.lengthoftime)
        end
    END;
    library.obsdetails[tempsubddetails.sd]:=tempsubddetails
end;
close(textfile);
displayln('... loading ends.',20,3);
displayln('A library is now loaded in memory',2,5);
if library.nrofentries = maxentries
then displayln('Library is FULL',5,6)
end;
Delay(500)
end; {load}

{-----}

PROCEDURE librarymenu (var library: librarytype);
{ ----- }

    var choice: char;

    begin
        REPEAT
            ClrScr;
            displayln('LIBRARY MENU',12,0);
            displayln('(1) Load in a previous library',6,2);
            displayln('(2) Display current library',6,3);
            displayln('(0) Quit and return to main menu',6,4);
            displayln('CHOICE ... ',12,5);
            getandcheckentry(24,5,choice,'0','2',2,7);
            CASE choice OF
                '1': load(library);
                '2': display(library)
            END
        UNTIL choice = '0';
        ClrScr;
        displayln('*** End of Library Session ***',5,3);
        Delay(1000)
    end; {librarymenu}

END.

{*****}

```

```
{*****}
```

```
UNIT Mbun_obs;  
( ===== )
```

```
INTERFACE
```

```
USES Mbun_typ;
```

```
PROCEDURE observation (library:librarytype);
```

```
IMPLEMENTATION
```

```
USES DIP_Crt,Dos,Mbun_gen,Mbun_lib;
```

```
PROCEDURE ex_getandcheckentry (x,y:byte; var inp:char; lwb,upb:char;  
( ----- ) a,b:byte; library:librarytype);
```

```
var keyid:entryidtype;  
OK: Boolean;
```

```
begin
```

```
OK:=false;
```

```
REPEAT
```

```
REPEAT
```

```
waitandgetchar(x,y,inp);
```

```
if ((NOT (inp in [lwb..upb])) OR (inp in ['!..''])) OR (inp = '-')  
OR (inp = '=') OR (inp = '@'))
```

```
AND (inp<>chr(CTRLS)) AND(inp<>chr(ESC))
```

```
then displayln('Incorrect entry - enter an alternative',a,b)
```

```
UNTIL (inp = chr(CTRLS)) OR (inp = chr(ESC)) OR
```

```
((inp in [lwb..upb]) AND (NOT (inp in ['!..'']))) AND
```

```
(inp<>'-' ) AND (inp<>'=' ) AND (inp<>'@' ));
```

```
if (inp<>chr(CTRLS)) AND (inp<>chr(ESC))
```

```
then begin
```

```
keyid:=inp;
```

```
if library.entries[keyid].key = '!'
```

```
then displayln('This key does not exist in the library',a,b)
```

```
else if library.entries[keyid].subdivision = '4'
```

```
then displayln('Key entry must be from s/d 1-3',a,b)
```

```
else OK:=true
```

```
end
```

```
UNTIL (OK) OR (inp = chr(CTRLS)) OR (inp = chr(ESC));
```

```
displayln(blankline,a,b)
```

```
end; {ex_getandcheckentry}
```

```
{-----}
```

```
PROCEDURE ex_getandcheckentry_cont (x,y:byte; var inp:char; lwb,upb:char;  
( ----- ) a,b:byte; library:librarytype;  
usingcounter:Boolean);
```

```
var keyid:entryidtype;  
OK: Boolean;
```

```
begin
```

```
OK:=false;
```

```
REPEAT
```

```
REPEAT
```

```
waitandgetchar(x,y,inp);
```

```

        if ((NOT (inp in [lwb..upb])) OR (inp in ['\..\'])) OR
            (inp in ['\..\']) OR
            (inp = '@') OR ((inp = '-') AND NOT usingcounter) OR
            ((inp = '=') AND NOT usingcounter) OR
            ((inp = ' ') AND NOT usingcounter) OR
            ((inp = chr(BACKSPACE)) AND NOT usingcounter))
            AND (inp<>chr(CTRLS)) AND(inp<>chr(ESC))
        then displayln('Incorrect entry - enter an alternative',a,b)
    UNTIL (inp = chr(CTRLS)) OR (inp = chr(ESC)) OR
        ((inp in [lwb..upb]) AND (NOT (inp in ['\..\'])))
            AND (NOT (inp in ['\..\'])) OR
        ((inp = '-') AND usingcounter) OR
        ((inp = '=') AND usingcounter) OR
        ((inp = ' ') AND usingcounter) OR
        ((inp = chr(BACKSPACE)) AND usingcounter) AND (inp<>'@'));
    if (inp<>chr(CTRLS)) AND (inp<>chr(ESC)) AND (inp <> '=') AND
        (inp <> '-') AND (inp <> chr(BACKSPACE)) AND (inp <> ' ')
        AND (inp <> chr(NUL))
    then begin
        keyid:=inp;
        if library.entries[keyid].key = '*'
        then displayln('This key does not exist in the library',a,b)
        else if library.entries[keyid].subdivision = '4'
            then displayln('Key entry must be from s/d 1-3',a,b)
            else OK:=true
        end
    UNTIL (OK) OR (inp = chr(CTRLS)) OR (inp = chr(ESC)) OR (inp = chr(NUL))
        OR ((inp = '-') AND usingcounter) OR
        ((inp = '=') AND usingcounter) OR
        ((inp = ' ') AND usingcounter) OR
        ((inp = chr(BACKSPACE)) AND usingcounter);
    displayln(blankline,a,b)
end; {ex_getandcheckentry}

(-----)

( PROCEDURE ex_getandcheckentry_con (x,y:byte; var inp:char; lwb,upb:char; )
( ----- ) ( a,b:byte; library:librarytype);)

( var keyid:entryidtype;

begin
    ex_getandcheckentry(x,y,inp,lwb,upb,a,b,library);
    if (inp <> chr(CTRLS)) AND (inp <> chr(ESC))
    then begin
        keyid:=inp;
        if (library.obsdetails[library.entries[keyid].subdivision].
            modeofrecording = timesampling)

        then begin
            displayln('This key is from a TIME SAMPLING s/d',1,8);
            delay(500);
            displayln(blankline,a,b)
        end
    end
end; )

(-----)

```

```

PROCEDURE ex_getandcheckentry_timesample (x,y:byte; var inp:char;
( ----- ) lwb,upb:char; a,b:byte;
library:librarytype;
subdiv:limitedsubdtype);

var keyid: entryidtype;

begin
  REPEAT
    REPEAT
      getandcheckentry(x,y,inp,firstentry,lastentry,1,8);
      keyid:=inp;
      if library.entries[keyid].key = '*'
      then displayln('This key does not exist in the library',1,8)
    UNTIL library.entries[keyid].key<>'*';
    if library.entries[keyid].subdivision <> subdiv
    then displayln('Wrong key for this time sampling s/d',1,8)
    UNTIL (library.entries[keyid].subdivision = subdiv);
    displayln(blankline,a,b)
  end;

(-----)

PROCEDURE displaytime (t:timetype;x,y:byte);
( ----- )

begin
  GotoXY(x,y);
  write(t.hours:2,':');
  if t.mins < 10
  then write('0');
  write(t.mins,':');
  if t.secs < 10
  then write('0');
  writeln(t.secs)
end;

(-----)

PROCEDURE writetimetodisk (var textfile:text; t:timetype);
( ----- )

begin
  write(textfile,t.hours:2,':');
  if t.mins < 10
  then write(textfile,'0');
  write(textfile,t.mins,':');
  if t.secs < 10
  then write(textfile,'0');
  write(textfile,t.secs)
end;

(-----)

```



```

PROCEDURE writedatetodisk (var textfile:text; d:datatype);
{ ----- }

begin
  write(textfile,d.day:2,' ');
  if d.month < 10
  then write(textfile,'0');
  write(textfile,d.month,':',d.year:4)
end;

{-----}

PROCEDURE addontime (var t:timetype; addedtime:word);
{ ----- }

var count:word;

begin
  t.secs:=t.secs + addedtime;
  count:=0;
  while t.secs >59 DO
    begin
      t.secs:=t.secs -60;
      count:=count+1
    end;
  t.mins:=t.mins + count;
  count:=0;
  while t.mins >59 DO
    begin
      t.mins:=t.mins -60;
      count:=count+1
    end;
  t.hours:=t.hours + count;
  if t.hours >23
  then t.hours:=t.hours -24
end; {addontime}

{-----}

FUNCTION firsttimegreaterorequal (t1,t2: timetype): Boolean;
{ ----- }

var value1,value2:word;

begin
  if (t1.hours = 0) AND (t2.hours = 24)
  then t1.hours:=t1.hours +24;
  value1:=t1.secs + (t1.mins *60) + (t1.hours *3600);
  value2:=t2.secs + (t2.mins *60) + (t2.hours *3600);
  firsttimegreaterorequal:=value1 >= value2
end;

{-----}

PROCEDURE setupscreendisplay (var x1,x2,x3,y1,y2,y3:byte; focalid:idtype;
{ ----- } library: librarytype);

begin
  clrscr;
  writeln('FOCAL ID:',focalid:3,' KEY PRESSED:');
  writeln('-----');

```

```

CASE nrofsubdivisions(library) OF
  1: begin          (set up screen display)
      x1:=10;
      y1:=4;
      displayln('(1)',4,2)
    end;
  2: begin
      x1:=2; x2:=22;
      y1:=3; y2:=4;
      displayln('(1)              (2)',4,2)
    end;
  3: begin
      x1:=2; x2:=23; x3:=22;
      y1:=3; y2:=2; y3:=5;
      displayln('(1)              (2)',4,2);
      displayln('(3)',19,5)
    end
END
end; {setupscreendisplay}

{-----}

PROCEDURE initializefile (obsfilename:string; sd:limitedsubdtype;
  { ----- }          t:timetype; d:datatype);

var
  textfile: text;

begin
  obsfilename:=(obsfilename + sd) + '.txt';
  assign(textfile,obsfilename);
  rewrite(textfile);
  write(textfile,'***          ');
  writetimetodisk(textfile,t);
  write(textfile,' ');
  writedatetodisk(textfile,d);
  writeln(textfile);
  close(textfile)
end; {initializefile}

{-----}

PROCEDURE closefile (obsfilename:string; sd:limitedsubdtype; t:timetype;
  { ----- }          d:datatype);

var
  textfile: text;

begin
  obsfilename:=(obsfilename + sd) + '.txt';
  assign(textfile,obsfilename);
  append(textfile);
  write(textfile,'...          ');
  writetimetodisk(textfile,t);
  write(textfile,' ');
  writedatetodisk(textfile,d);
  writeln(textfile);
  close(textfile)
end; {closefile}

{-----}

```

```

PROCEDURE storeobservation (obsfilename:string; sd:limitedsubtype;
{ ----- } id:idtype; observation:observationtype;
                                obsdetails: obsdetailtype; d: datatype);

var
    textfile: text;
    spaces: integer;

begin
    obsfilename:=(obsfilename + sd) + '.txt';
    assign(textfile,obsfilename);
    append(textfile);
    WITH observation DO
        begin
            write(textfile,id:3,' ',k,' ',promptedinfo);
            spaces:=(maxpromptedinfo - Length(promptedinfo)) +1;
            write(textfile,' ':spaces);
            if obsdetails[sd].modeofrecording = continuous
            then begin
                writetimetodisk(textfile,time);
                write(textfile,' ');
                writedatetodisk(textfile,d);
                write(textfile,' ')
            end;
            if obsdetails[sd].extrasubd <>'0'
            then write(textfile,extrak,' ',extrapromptedinfo);
            if nrofbytes <> 0
            then begin
                spaces:=(maxpromptedinfo - Length(extrapromptedinfo)) +1;
                writeln(textfile,' ':spaces,nrofbytes)
            end
            else writeln(textfile)
            end;
        close(textfile)
    end; {storeobservation}

{-----}

PROCEDURE makeobs (obsfilename:string; inp:char; currentsd:limitedsubtype;
{ ----- } t:timetype; var firsttime:Boolean;
                                library:librarytype; var obs:obstype; focalid:idtype;
                                d:datatype; x,y:byte; countingkey:char);

var
    temp:char;
    tempstring: ARRAY [1..6] OF char;
    keyid:entryidtype;
    OK:Boolean;
    i,position:byte;

begin
    displaytime(t,16,0);
    if (NOT firsttime) AND (inp <> ' ') AND (inp <> '-') AND (inp<>'=')
        AND (inp <> chr(BACKSPACE))
    then storeobservation(obsfilename,currentsd,focalid,obs[currentsd],
                                library.obsdetails,d)
    else firsttime:=FALSE;

```

```

WITH library DO
  if (inp = ' ') OR (inp = '-') OR (inp = '=') OR (inp = chr(BACKSPACE))
  then obs[currentsd].nrofbites:=obs[currentsd].nrofbites +1
  else begin
    obs[currentsd].k:=inp;
    displayln('          ',x,y);
    displayln(entries[inp].description,x,y);
    if obsdetails[currentsd].extrasubd <> '0'
  {
      then begin
        obs[currentsd].extrak:='-';
        obs[currentsd].extrapromptedinfo:='---'
      end )
    then begin
      obs[currentsd].extrak:=obs[obsdetails[currentsd].
                                extrasubd].k;

      obs[currentsd].extrapromptedinfo:=
        obs[obsdetails[currentsd].extrasubd].promptedinfo
    end;
    if obsdetails[currentsd].modeofrecording = continuous
    then obs[currentsd].time:=t;
    GotoXY(x-2,y+1);
    displayln('          ',x-2,y+1);
    displayln('          ',x+2,y+2);
    if entries[inp].prompt
    then begin
      displayln(entries[inp].promptinfo,x-2,y+1);
      obs[currentsd].promptedinfo:='';
      temp:=Readkey;
      if temp = chr(ESC)
      then begin
        OK:=FALSE;
        REPEAT
          getafterRETURNandcheckentry(x+2,y+2,temp,
                                firstentry,lastentry,0,7);

          keyid:=temp;
          if entries[keyid].key = '*'
          then displayln('This key does not exist in the library',0,7)
          else if entries[keyid].subdivision <> '4'
            then displayln('Key entry must be from s/d 4',0,7)
            else OK:=TRUE
        UNTIL OK;
        displayln(blankline,0,7);
        displayln(entries[keyid].description,x+2,y+2);
        obs[currentsd].promptedinfo:=entries[keyid].description
      end
    else begin
      FOR i:=1 to 6 DO
        tempstring[i]:=' ';
      GotoXY(x+2,y+2);
      position:=x+2;
    end
  end
end

```

```

REPEAT
  if temp <> chr(RETURN)
  then begin
    if temp = chr(BACKSPACE)
    then begin
      if position > x+2
      then begin
        position:=position-1;
        GotoXY(position,y+2);
        write(' ':1);
        tempstring[position-(x+1)]:= ' '
      end
    end
    else if position < ((x+2)+maxpromptedinfo)
    then begin
      GotoXY(position,y+2);
      write(temp:1);
      tempstring[position-(x+1)]:=temp;
      position:=position+1
    end;
    if position = ((x+2)+maxpromptedinfo)
    then write(chr(BELL));
    temp:=Readkey
  end
  else if position = x+2
  then begin
    displayln('Make an entry!',1,7);
    Delay(500);
    displayln(blankline,0,7);
    temp:=Readkey
  end
  UNTIL ((temp=chr(RETURN)) AND (position >x+2));
  obs[currentsd].promptedinfo:=tempstring
end

end
else obs[currentsd].promptedinfo:='-';
if obs[currentsd].k = countingkey
then obs[currentsd].nrofbytes:= 1
else obs[currentsd].nrofbytes:=0
end
end; {makeobs}

{-----}

PROCEDURE dealwithESC (obsfilename:string; currentsd:char; var obs:obstype;
{ ----- } library:librarytype; firsttime:Boolean;
focalid:idtype; d:datatype; x,y:byte;
var usingcounter:Boolean; countingkey:char);

var
  inp:char;

begin
  displayln('CTRL-E: Error; CTRL-P: Prompt; ESC: Cont',0,7);
  REPEAT
    waitandgetchar(39,0,inp)
  UNTIL (inp = chr(CTRLE)) OR (inp = chr(CTRLP)) OR (inp = chr(ESC));

```

```

CASE inp OF
  chr(CTRLE): begin
    storeobservation(obsfilename, currentsd,errorid,
                     obs[currentsd],library.obsdetails,d);
    displayln(blankline,0,7);
    displayln('Enter replacement key etc ... OR ESC',1,7);
    ex_getandcheckentry(39,0,inp,firstentry,lastentry,
                        0,7,library);
    if (inp <> chr(ESC)) AND (inp <> chr(CTRLS))
    then begin
      firsttime:=(library.entries[inp].subdivision=
                  currentsd);

      if inp=countingkey
      then usingcounter:=TRUE
      else if (library.entries[inp].subdivision =
              library.entries[countingkey].subdivision)
      then usingcounter:= FALSE;
      makeobs(obsfilename,inp,
              library.entries[inp].subdivision,
              obs[currentsd].time,firsttime,library,
              obs,focalid,d,x,y,
              countingkey)
    end
  end;
  chr(CTRLP): begin
    displayln(blankline,0,7);
    displayln('Enter replacement prompted info ...',1,7);
    GotoXY(x+2,y+2);
    readln(obs[currentsd].promptedinfo)
  end
END;
displayln(blankline,0,7)
end; {dealwithESC}

(-----)

PROCEDURE doobservation (obsfilename:string; var t:timetype;
( ----- ) library:librarytype; var bleeps:bleepstype;
var inp:char; var firsttime1,firsttime2,
firsttime3:Boolean; var obs:obstype;
focalid:idtype; d:datetype; x1,x2,x3,y1,y2,y3:
byte; countingkey:char; var usingcounter:Boolean);

var
  i,proposedsd,currentsd:char;
  hunds:word;
  previoustime:timetype;
  x,y: byte;

begin
  previoustime:=t;
  gettime(t.hours,t.mins,t.secs,hunds);
  if t.mins <> previoustime.mins
  then displaytime(t,16,0);

```

```

FOR i:= '1' TO '3' DO {check each time sampling s/d to see}
  WITH library.obsdetails[i] DO {if time}
    if (sd <> '*') AND (modeofrecording = timesampling)
      then if firsttimegreaterorequal(t,bleeps[i]) {it is time}
        then begin
          write(chr(BELL));
          addontime(bleeps[i],lengthoftime);
          ex_getandcheckentry_timesample(39,0,inp,firstentry,
                                          lastentry,1,7,library,i);

          CASE i OF
            '1': makeobs(obsfilename,inp,i,t,firsttime1,library,
                          obs,focalid,d,x1,y1,
                          countingkey);
            '2': makeobs(obsfilename,inp,i,t,firsttime2,library,
                          obs,focalid,d,x2,y2,
                          countingkey);
            '3': makeobs(obsfilename,inp,i,t,firsttime3,library,
                          obs,focalid,d,x3,y3,
                          countingkey)

          END
        end;
    if Keypressed {check to see if a key has been pressed}
      then begin
        gettime(t.hours,t.mins,t.secs,hunds);
        ex_getandcheckentry_cont(39,0,inp,firstentry,lastentry,
                                1,7,library,usingcounter);

        if inp <> chr(NUL)
          then
            if inp = chr(ESC)
              then begin
                displayln('Enter s/d you want to deal with ...',1,7);
                getandcheckentry(39,0,proposedsd,'1','3',1,7);
                CASE proposedsd OF
                  '1': if firsttime1
                      then begin
                        displayln
                          ('No observation has been made for this s/d yet'
                           ,1,7);

                        Delay(500)
                      end
                  else dealwithESC(obsfilename,'1',obs,library,
                                firsttime1,focalid,d,x1,y1,
                                usingcounter,countingkey);
                  '2': if firsttime2
                      then begin
                        displayln
                          ('No observation has been made for this s/d yet'
                           ,1,7);

                        Delay(500)
                      end
                  else dealwithESC(obsfilename,'2',obs,library,
                                firsttime2,focalid,d,x2,y2,
                                usingcounter,countingkey);
                END
              end
            end
          end
      end
    end
  end

```

```

'3': if firsttime3
then begin
    displayln
    ('No observation has been made for this s/d yet'
    ,1,7);
    Delay(500)
end
else dealwithESC(obsfilename,'3',obs,library,
    firsttime1,focalid,d,x3,y3,
    usingcounter,countingkey)
END
end
else if (inp <> chr(CTRLS))
then begin
    if inp = countingkey
    then usingcounter:=TRUE;
    if ((inp = ' ') OR (inp = '=') OR (inp = '-') OR
        (inp = chr(BACKSPACE)) OR (inp = countingkey))
    then currentsd:=library.entries[countingkey].
        subdivision
    else begin
        currentsd:=library.entries[inp].subdivision;
        if (library.entries[inp].subdivision =
            library.entries[countingkey].subdivision)
        then usingcounter:=FALSE
    end;
CASE currentsd OF
'1':makeobs(obsfilename,inp,currentsd,
    t,firsttime1,library,obs,focalid,d,x1,y1,
    countingkey);
'2':makeobs(obsfilename,inp,currentsd,
    t,firsttime2,library,obs,focalid,d,x2,y2,
    countingkey);
'3':makeobs(obsfilename,inp,currentsd,
    t,firsttime3,library,obs,focalid,d,x3,y3,
    countingkey)
END;
if library.entries[inp].description = 'out_of_sight'
then FOR i:='1' to '3' DO
    if i <> library.entries[inp].subdivision
    then begin
        storeobservation(obsfilename,i,focalid,
            obs[i],library.obsdetails,d);
        obs[i].time:=t;
        obs[i].k:=inp;
        CASE i OF
        '1': begin
            x:=x1;
            y:=y1
        end;
        '2': begin
            x:=x2;
            y:=y2
        end;
        '3': begin
            x:=x3;
            y:=y3
        end
    end
END;

```



```

displayln(' ',x,y);
displayln('NB.out_of_sight',x,y);
obs[i].promptedinfo:='-';
obs[i].nrofbytes:=0
end
end
end; {doobservation}

{-----}

PROCEDURE observation (library:librarytype);
{ ----- }

var
  obsfilename:string;
  focalid: idtype;
  d:datatype;
  t,stoptime,bleeptime:timetype;
  dofwhunds,timesamplestagger:word;
  i,inp,countingkey:char;
  x1,x2,x3,y1,y2,y3:byte;
  usingcounter:Boolean;
  bleeps: bleepstype;
  obs:obstype;
  firsttime1,firsttime2,firsttime3:Boolean;
  count,count1:integer;

begin
  clrscr;
  displayln('OBSERVATION',13,0);
  Delay(500);
  if library.nrofentries = 0
  then begin
    displayln('A library of behaviours is necessary for',0,2);
    displayln('observation - please enter one.',0,3);
    Delay(500)
  end
  else begin
    displayln('Enter name of file to store',2,2);
    displayln('observations - 1 to 6 chars -- <RET>',0,3);
    REPEAT
      REPEAT
        GotoXY(9,4);
        obsfilename:='';
        readln(obsfilename);
        if Length(obsfilename) > 6
        then begin
          displayln('Filename too long - try again',0,7);
          delay(500);
          displayln(blankline,0,4);
          displayln(blankline,0,7)
        end
      UNTIL Length(obsfilename) <= 6;
      obsfilename:=('A:' + obsfilename) + '_';

```

```

if (fileexists(obsfilename + '1.txt'))
  OR (fileexists(obsfilename + '2.txt'))
  OR (fileexists(obsfilename + '3.txt'))
then begin
  displayln('This file already exists - try again',0,7);
  Delay(500);
  displayln(blankline,0,4);
  displayln(blankline,0,7)
end
UNTIL (NOT (fileexists(obsfilename + '1.txt'))) AND
      (NOT (fileexists(obsfilename + '2.txt'))) AND
      (NOT (fileexists(obsfilename + '3.txt')));
displayln('Enter focal animal id (->3chrs) -- <RET>',0,6);
GotoXY(9,7);
readln(focalid);
getdate(d.year,d.month,d.day,dofw);
setupscreendisplay(x1,x2,x3,y1,y2,y3,focalid,library);
gettime(t.hours,t.mins,t.secs,hunds);
displaytime(t,16,0);
displayln('Press any key to start ...',1,7);
waitandgetchar(29,7,inp);
displayln(blankline,0,7);
REPEAT
  gettime(t.hours,t.mins,t.secs,hunds)
UNTIL t.secs = 0;
displaytime(t,16,0);
write(chr(BELL));
timesamplestagger:=0;
FOR i:='1' TO '3' DO
  WITH library.obsdetails[i] DO
    if sd <> '*' {if the s/d exists}
    then begin
      initializefile(obsfilename,sd,t,d);
      if modeofrecording = timesampling
      then begin {calculate first bleep time}
        bleeptime:=t;
        addontime(bleeptime,lengthoftime);
        addontime(bleeptime,timesamplestagger);
        bleeps[i]:=bleeptime; {store it in the var.}
        timesamplestagger:=timesamplestagger + 30
      end;
      obs[i].k:='-'; {initialize k & promptedinfo values}
      obs[i].promptedinfo:='-';
    end;
  stoptime:=t;
  addontime(stoptime,lengthofobsession); {calculate stop time}
  firsttime1:=TRUE;
  firsttime2:=TRUE;
  firsttime3:=TRUE;
  inp:='!';
  countingkey:=countkey;
  usingcounter:=FALSE;
  REPEAT {ie do observations till stop}
    doobservation(obsfilename,t,library,bleeps,inp,firsttime1,
      firsttime2,firsttime3,obs,focalid,d,
      x1,x2,x3,y1,y2,y3,countingkey,usingcounter)
  UNTIL (firsttimegreaterorequal(t,stoptime)) OR (inp=chr(CTRLS));
  write(chr(BELL));
  Delay(300);
  write(chr(BELL));
  count:=0;

```

```

FOR i:='1' TO '3' DO
  if library.obsdetails[i].sd <> '*'
  then begin
    CASE i OF
      '1': if NOT firsttime1
        then storeobservation(obsfilename,i,focalid,obs[i],
          library.obsdetails,d);
      '2': if NOT firsttime2
        then storeobservation(obsfilename,i,focalid,obs[i],
          library.obsdetails,d);
      '3': if NOT firsttime3
        then storeobservation(obsfilename,i,focalid,obs[i],
          library.obsdetails,d)
    END;
    if inp = chr(CTRLS)
    then begin
      gettime(t.hours,t.mins,t.secs,hunds);
      closefile(obsfilename,i,t,d)
    end
    else closefile(obsfilename,i,stoptime,d)
    end;

(
      else if library.obsdetails[i].modeofrecording =
        timesampling
      then begin
        closefile(obsfilename,i,stoptime,d);
        count:=count+1
      end
      else displayln
        ('End behavs. being recorded by cont. s/ds',
          1,7)
    end;
  if inp <> chr(CTRLS)
  then while count <> nrofsubdivisions(library) DO
    begin
      count1:=count;
      REPEAT
        ex_getandcheckentry(39,0,inp,firstentry,lastentry,
          1,7,library);
        if (inp = chr(CTRLS)) OR (inp = chr(ESC))
        then displayln('Inappropriate entry here',1,7)
      UNTIL (inp <> chr(CTRLS)) AND (inp <> chr(ESC));
      FOR i:='1' TO '3' DO
        if (library.obsdetails[i].sd <> '*') AND
          (library.obsdetails[i].modeofrecording = continuous)
          AND (obs[i].k <> '*')
        then if obs[i].k = inp
          then begin
            gettime(t.hours,t.mins,t.secs,hunds);
            closefile(obsfilename,i,t,d);
            obs[i].k:='*';
            count:=count+1;
            displayln('A continuous subdivision ended',
              4,7);

            Delay(2000)
          end;
    end;
  end;

```

```
        if count = count1
        then displayln('Incorrect entry - must be the same key',1,7)
        end; }

        displayln('    *** End of Observations ***',1,7);
        Delay(1000)
    end
end; {observation}

END.
```

```
{*****}
```

```
{*****}
```

```
UNIT Mbun_loc;  
{ ===== }
```

```
INTERFACE
```

```
PROCEDURE location;
```

```
IMPLEMENTATION
```

```
USES DIP_Crt,Dos,Mbun_typ,Mbun_gen;
```

```
PROCEDURE storelocinfo (gridref:longint; distance:real);  
{ ----- }
```

```
var  
  textfile:text;  
  t:timetype;  
  d:datetype;  
  hunds,dofw:word;  
  
begin  
  getdate(d.year,d.month,d.day,dofw);  
  gettime(t.hours,t.mins,t.secs,hunds);  
  if NOT (fileexists(locfilename))  
  then begin  
    assign(textfile,locfilename);  
    rewrite(textfile)  
  end  
  else begin  
    assign(textfile,locfilename);  
    append(textfile)  
  end;  
  write(textfile,gridref:6,' ',t.hours:2,':',t.mins:2,':',t.secs:2);  
  write(textfile,' ',d.day:2,':',d.month:2,':',d.year:4,' ');  
  writeln(textfile,distance:6:0);  
  close(textfile)  
end; {storelocinfo}
```

```
{-----}
```

```
PROCEDURE entergridref;  
{ ----- }
```

```
var  
  newgridref,oldgridref:longint;  
  previousdistance,distancetravelled,x,y,runningtotal: real;  
  textfile: text;  
  junk: string[21];  
  
begin  
  clrscr;  
  displayln('Enter the 6 figure grid reference:',2,2);
```

```

REPEAT
    enterpositivenumber(10,4,newgridref,6);
    if newgridref <= 99999
    then begin
        displayln('Grid ref. should be 6 figures -try again',1,6);
        displayln(blankline,1,4)
    end
UNTIL newgridref > 99999;
displayln(blankline,1,6);
if NOT (fileexists(locfilename))
then storelocinfo(newgridref,0)
else begin
    assign (textfile,locfilename);
    reset(textfile);
    while (NOT eof(textfile)) DO
        readln(textfile,oldgridref,junk,previousdistance);
    close(textfile);
    x:=abs((newgridref DIV 1000) - (oldgridref DIV 1000));
    y:=abs((newgridref MOD 1000) - (oldgridref MOD 1000));
    distancetravelled:=((sqrt(sqr(x) + sqr(y))) * (100));
    runningtotal:=previousdistance + distancetravelled;
    storelocinfo(newgridref,runningtotal)
end;
displayln('Entered on file and calculations made',1,6);
Delay(2000)
end; {entergridref}

{-----}

PROCEDURE displaylocinfo;
( ----- )

var textfile: text;
    oneline: string[40];
    cha:char;

begin
    ClrScr;
    if NOT (fileexists(locfilename))
    then displayln('No entries have been made yet.',1,4)
    else begin
        displayln('The current location information is :',1,2);
        assign(textfile,locfilename);
        reset(textfile);
        while (NOT eof(textfile)) DO
            readln(textfile,oneline);
        displayln(oneline,1,4)
    end;
    displayln('Press any key to continue ...',4,6);
    waitandgetchar(34,6,cha)
end; {displaylocinfo}

{-----}

```

```

PROCEDURE location;
( ----- )

var choice:char;

begin
  REPEAT
    clrscr;
    displayln('LOCATION MENU',14,0);
    displayln('(1) Enter new grid location',6,2);
    displayln('(2) Display previous location and',6,3);
    displayln('distance travelled so far.',4,4);
    displayln('(0) Quit and return to main menu',6,5);
    displayln('CHOICE',12,6);
    getandcheckentry(20,6,choice,'0','2',0,7);
  CASE choice OF
    '1': entergridref;
    '2': displaylocinfo
  END
  UNTIL choice = '0'
end;

END.

(*****)
```

```
{*****}
```

```
PROGRAM Mb_libry;  
{ ===== }
```

```
USES DIP_Crt,Dos,  
      Mbun_typ,Mbun_gen;
```

```
VAR  
  library:librarytype;  
  junk:char;
```

```
{-----}
```

```
PROCEDURE initializelibrary (var library:librarytype);  
{ ----- }
```

```
  var i:char;  
  
  begin  
    FOR i:= firstentry TO lastentry DO  
      library.entries[i].key:='*';  
      library.nrofentries:=0;  
      FOR i:= '1' TO '3' DO  
        library.obsdetails[i].sd:='*'  
      end;  
  end;
```

```
{-----}
```

```
PROCEDURE enterkey (library:librarytype; var tempentry: lentrytype);  
{ ----- }
```

```
  var inp:char;  
  
  begin  
    displayln('Key (A-Z,a-z,0-9,etc.) -- RETURN :',3,1);  
    REPEAT  
      getafterRETURNandcheckentry(39,1,inp,firstentry,lastentry,2,8);  
      if library.entries[inp].key <> '*'  
      then displayln('Already an entry for that key -try again',1,8)  
    UNTIL library.entries[inp].key = '*';  
    displayln(blankline,1,8);  
    tempentry.key:=inp  
  end; {enterkey}
```

```
{-----}
```

```
PROCEDURE enterdescription (var tempentry:lentrytype);  
{ ----- }
```

```
  var tempstring:string[18];  
  
  begin  
    displayln('Description (<18 chrs,no spaces) --<RET>',1,2);  
    GotoXY(4,3);  
    readln(tempstring);  
    tempentry.description:=tempstring  
  end;
```

```
{-----}
```



```

PROCEDURE enterprompt (var tempentry: lentrytype);
{ ----- }

var
    inp:char;
    tempstring:string[15];

begin
    displayln('Do you wish to prompt for any additional',1,4);
    displayln('information to be stored for this key?',1,5);
    waitforyorn(40,5,inp);
    if (inp = 'Y') OR (inp = 'y')
    then begin
        tempentry.prompt:=TRUE;
        displayln('Enter the prompt ( <15 chars) -- RETURN',1,6);
        GotoXY(4,7);
        readln(tempstring);
        tempentry.promptinfo:=tempstring
    end
    else tempentry.prompt:=FALSE;
    Delay(2000)
end;

{-----}

PROCEDURE makeanentry (var library:librarytype; subdiv: subdivisiontype);
{ ----- }

var
    inp: char;
    tempentry: lentrytype;

begin
    displayln('Enter key identity & following details:',1,4);
    Delay(2000);
    ClrScr;
    enterkey(library,tempentry);
    enterdescription(tempentry);
    enterprompt(tempentry);
    displayln('*** RECORD this entry? Y/N',1,8);
    waitforyorn(29,8,inp);
    if (inp = 'Y') OR ( inp = 'y')
    then begin
        tempentry.subdivision:=subdiv;
        library.entries[tempentry.key]:=tempentry;
        library.nrofentries:=library.nrofentries + 1
    end
end; {makeanentry}

{-----}

PROCEDURE displaysubdivisionblurb;
{ ----- }

var inp:char;

begin
    ClrScr;
    displayln('Up to 3 subdivisions of the library into',1,1);
    displayln('mutually exclusive sets of behaviours',1,2);
    displayln('can be made',1,3);

```

```

displayln('A fourth s/d can be used for entries',3,4);
displayln('in the library for which no time record',1,5);
displayln('is needed ie those which are to be used',1,6);
displayln('only as a short-hand.',1,7);
displayln('Press any key to continue',5,8);
waitandgetchar(30,8,inp);
ClrScr;
displayln('For each library entry, view the info.',3,1);
displayln('already recorded and enter the sub/d',1,2);
displayln('(1-4) that the entry should belong to.',1,3);
displayln('Press any key to continue ... ',4,6);
waitandgetchar(34,6,inp)
end;

```

(-----)

```

PROCEDURE allocatesubdivisions (var library: librarytype);
( ----- )

```

```

var inp,i:char;

begin
  ClrScr;
  displayln('key description      prompt      s/d',1,1);
  FOR i:=firstentry TO lastentry DO
    WITH library.entries[i] DO
      if key <> '*'
      then begin
        displayln(key,2,3);  (present library entry so far)
        displayln(description,4,3);
        if prompt
        then displayln(promptinfo,23,3);
        displayln('Enter the subdivision that this entry',1,5);
        displayln('will belong to (1-4) -- RETURN.',1,6);
        getafterRETURNandcheckentry(39,3,inp,'1','4',1,8);
        subdivision:=inp;
        if inp in ['1'..'3']
        then if library.obsdetails[inp].sd = '*'
              then library.obsdetails[inp].sd:=inp;
        Delay(2000);
        displayln(blankline,1,3)
      end
    end; (allocatesubdivisions)

```

(-----)

```

FUNCTION timelength: integer;
( ----- )

```

```

var period:longint;

begin
  displayln('Enter the time interval for the beep',3,5);
  displayln('for time sampling, in seconds',1,6);
  displayln('Time interval:',5,7);
  REPEAT
    enterpositivenumber(21,7,period,4);
    if period = 0
    then displayln('Time length cannot be zero',1,8)
  UNTIL period <> 0;
  displayln(blankline,1,8);
  timelength:=period;

```

```

        Delay(1000);
        displayln(blankline,1,6);
        displayln(blankline,1,7);
        displayln(blankline,1,8)
    end; {timelength}

{-----}

PROCEDURE entermodeofrecording (var subdinfo: subddetailstype;
{ ----- }                          subdiv:char);

    var inp: char;

    begin
        GotoXY(1,4);
        writeln('          ',subdiv,':--');
        REPEAT
            waitandgetchar(16,4,inp)
        UNTIL (inp = 'T') OR (inp = 't') OR (inp = 'C') OR (inp = 'c');
        CASE inp OF
            'T','t': begin
                subdinfo.modeofrecording:=timesampling;
                subdinfo.lengthoftime:=timelength
            end;
            'C','c': subdinfo.modeofrecording:=continuous
        END;
        Delay(2000);
        displayln(blankline,1,4)
    end; {entermodeofrecording}

{-----}

PROCEDURE allocatemodeofrecording (var library: librarytype);
{ ----- }

    var
        i: limitedsubdtype;

    begin
        ClrScr;
        displayln('For each subdivision displayed',3,1);
        displayln('enter T or C for that s/d to use time',1,2);
        displayln('sampling or continuous mode of recording',1,3);
        Delay(1000);
        FOR i:=1 TO 3 DO
            if library.obsdetails[i].sd <> '*'
            then entermodeofrecording(library.obsdetails[i],
                                     library.obsdetails[i].sd)
        end; {allocatemodeofrecording}

{-----}

PROCEDURE initializeextrasubdtypedefault (var obsinfo: obsdetailstype);
{ ----- }

    var i: char;

    begin
        FOR i:=1 TO 3 DO
            if obsinfo[i].sd <> '*'
            then obsinfo[i].extrasubd:=defaultextrasubd
        end;

```

{-----}

```
FUNCTION nrofsubdivisions (library:librarytype): integer;  
{ ----- }
```

```
    var count: integer;  
        i: char;  
  
    begin  
        count:=0;  
        FOR i:='1' TO '3' DO  
            if library.obsdetails[i].sd <> '*'  
                then count:=count+1;  
            nrofsubdivisions:=count  
        end;
```

{-----}

```
PROCEDURE checkandenterextrasubd (var library:librarytype; primarysd: char);  
{ ----- }
```

```
    var extrasd:char;  
  
    begin  
        REPEAT  
            getafterRETURNandcheckentry(22,7,extrasd,'0','3',1,8);  
            if extrasd = primarysd  
                then displayln('Nonsense - duplication of data!',1,8)  
            else if extrasd = '0'  
                then library.obsdetails[primarysd].extrasubd:=extrasd  
            else if library.obsdetails[extrasd].sd = '*'  
                then displayln('This s/d is not being used.',1,8)  
            else if library.obsdetails[extrasd].  
                                modeofrecording = timesampling  
                then displayln  
                    ('Cannot take data from a time sample s/d',1,8)  
                else library.obsdetails[primarysd].extrasubd:=extrasd;  
            Delay(2000);  
            displayln(' ',22,7);  
            displayln(blankline,1,8)  
        UNTIL library.obsdetails[primarysd].extrasubd = extrasd;  
        displayln('OK - entry recorded.',4,8);  
        Delay(2000);  
        displayln(blankline,1,8)  
    end; {checkandenterextrasubd}
```

{-----}

```
PROCEDURE allocateextrasubds (var library: librarytype);  
{ ----- }
```

```
    var  
        primarysd:char;  
  
    begin  
        ClrScr;  
        displayln('For each subdivision as required',3,1);  
        displayln('enter the primary s/d first -- RETURN',1,2);  
        displayln('& then the s/d from which info should be',1,3);  
        displayln('recorded simultaneously -- RETURN',1,4);  
        displayln('(Enter 0 <RET> to finish)',3,5);
```

```

REPEAT
  getafterRETURNandcheckentry(15,7,primarysd,'0','3',1,8);
  if primarysd <> '0'
  then begin
    if library.obsdetails[primarysd].sd = '*'
    then displayln('This subdivision is not being used',1,8)
    else begin
      displayln('  ',16,7);
      checkandenterextrasubd(library,primarysd)
    end;
    Delay(2000);
    displayln(blankline,1,7);
    displayln(blankline,1,8)
  end
  UNTIL primarysd = '0'
end; (allocateextrasubds)

{-----}

PROCEDURE storelibrary (library:librarytype);
{ ----- }

var
  i:char;
  textfile: text;
  stringlength,spaces: integer;

begin
  assign(textfile,libfilename);
  rewrite(textfile);
  FOR i:=firstentry TO lastentry DO
    WITH library.entries[i] DO
      if key <> '*'
      then begin
        write(textfile,key,' ',description);
        stringlength:=Length(description);
        spaces:=(maxdescription - stringlength) +1;
        write(textfile,' ':spaces);
        write(textfile,subdivision);
        if prompt
        then writeln(textfile,' ',promptinfo)
        else writeln(textfile)
      end;
      writeln(textfile,'#');
      FOR i:='1' TO '3' DO
        WITH library.obsdetails[i] DO
          if sd <> '*'
          then begin
            write(textfile,sd,' ',extrasubd,' ');
            if modeofrecording = continuous
            then writeln(textfile,'continuous')
            else writeln(textfile,'timesample ',lengthoftime:5)
          end;
        Close(textfile)
      end; (storelibrary)

{-----}

PROCEDURE create (var library:librarytype);
{ ----- }

var inp:char;

```

```

begin
  ClrScr;
  inp:='1';
  if library.nrofentries <> 0 {if there already exists entries}
  then begin
    displayln('There already exists a library which',1,2);
    displayln('will be destroyed if a new one created',1,3);
    displayln('CONTINUE ... ? Y/N',5,5);
    waitforyorn(30,5,inp);
    if (inp = 'Y') OR (inp = 'y')
    then initializelibrary(library);
    ClrScr
  end;
  if (inp<>'N') AND (inp<>'n')
  then begin
    REPEAT
      makeanentry(library,defaultsubd);
      ClrScr;
      displayln('FINISHED making entries to the library',1,2);
      waitforyorn(40,2,inp)
    UNTIL (inp='Y') OR (inp='y') OR
      (library.nrofentries = maxentries);
    library.obsdetails[defaultsubd].sd:=defaultsubd;
    ClrScr;
    if library.nrofentries = maxentries
    then displayln('Library is FULL - no more entries added',1,1);
    if library.nrofentries > 1
    then begin
      displayln('Do you wish to subdivide the library?',1,3);
      waitforyorn(39,3,inp);
      if (inp = 'Y') OR (inp = 'y')
      then begin
        displaysubdivisionblurb;
        allocatesubdivisions(library)
      end
    end;
    ClrScr;
    displayln('Indicate the mode(s) of recording to be',1,2);
    displayln('used for the library ---',1,3);
    displayln('(An undivided library is subdivision 1)',1,4);
    Delay(3000);
    allocatemodeofrecording(library);
    initializeextrasubdtodefault(library.obsdetails);
    if nrofsubdivisions(library) > 1
    then begin
      ClrScr;
      displayln('Do you wish information from two s/d s',1,2);
      displayln('to be recorded simultaneously?',1,3);
      waitforyorn(32,3,inp);
      if (inp = 'Y') OR (inp = 'y')
      then allocateextrasubds(library)
    end;
    ClrScr;
    displayln('End of creating a library',5,4);
    displayln('Library is automatically stored on disk',1,6);
    storelibrary(library);
    Delay(3000)
  end
end; {create}

```

(-----)

```

PROCEDURE displayoneentry (entry: lentrytype; y:byte);
( ----- )

begin
  WITH entry DO
    begin
      displayln(key,1,y);
      displayln(description,3,y);
      displayln(subdivision,22,y);
      if prompt
        then displayln(promptinfo,26,y)
      end
    end
  end; { displayoneentry}

(-----)

PROCEDURE displayentries (library:librarytype);
( ----- )

const
  starty = 2;
  maxy = 7;

var
  y: byte;
  i,junk: char;

begin
  ClrScr;
  displayln('K Description      S/d   Prompt      ',1,1);
  y:=starty;
  FOR i:=firstentry TO lastentry DO
    begin
      if (library.entries[i].key <> '*') AND (y <> maxy)
        then begin
          displayoneentry(library.entries[i],y);
          y:=y+1
        end;
      if y = maxy
        then begin
          displayln('Press any key to continue ...',1,8);
          waitandgetchar(31,8,junk);
          ClrScr;
          displayln
            ('K Description      S/d   Prompt      ',1,1);
          y:=starty
        end
      end;
    end
  displayln('End of library',12,y);
  displayln('Press any key to continue ...',1,8);
  waitandgetchar(31,8,junk)
end; {displayentries}

(-----)

PROCEDURE displaysubddetails (library:librarytype);
( ----- )

const starty = 2;

```

```

var
  i:char;
  y:byte;

begin
  ClrScr;
  displayln('S/d Extra s/d Mode of rec. Length of tm.',1,1);
  y:=starty;
  FOR i:='1' TO '3' DO
    WITH library.obsdetails[i] DO
      if sd <> '*'
      then begin
        displayln(sd,2,y);
        displayln(extrasubd,6,y);
        if modeofrecording = continuous
        then displayln('continuous',15,y)
        else begin
          displayln('timesample',15,y);
          GotoXY(28,y);
          writeln(lengthoftime:5)
        end;
        y:=y+1
      end;
      displayln('Press any key to continue ...',1,6);
      waitandgetchar(31,6,i)
    end; {displaysubddetails}

{-----}

PROCEDURE display (library:librarytype);
{ ----- }

var choice:char;

begin
  ClrScr;
  if library.nrofentries = 0
  then begin
    displayln('There are no entries in the library',3,4);
    Delay(3000)
  end
  else REPEAT
    ClrScr;
    displayln('DISPLAY MENU',12,1);
    displayln('(1) Display library entries',6,2);
    displayln('(2) Display details about the',6,3);
    displayln('subdivisions used during observation',4,4);
    displayln('(0) Quit and return to library menu',6,5);
    displayln('CHOICE ...',12,6);
    getandcheckentry(24,6,choice,'0','2',1,8);
    CASE choice OF
      '1': displayentries(library);
      '2': displaysubddetails(library)
    END
    UNTIL choice = '0'
  end; {display}

{-----}

```



```

PROCEDURE Load (var library:librarytype);
( ----- )

var
    textfile:text;
    inp:char;
    tempentry:lentrytype;
    i:byte;
    tempsubdetails:subddetailstype;
    recordingmode:char;

begin
    ClrScr;
    inp:='!';
    assign(textfile,libfilename);
    if library.nrofentries <> 0
    then begin
        displayln('The current library in memory',1,2);
        displayln('will be overwritten',1,3);
        displayln('CONTINUE ... ? Y/N',5,5);
        waitforyorn(30,5,inp);
        if (inp = 'Y') OR (inp = 'y')
        then initializelibrary(library);
        ClrScr
    end;
    if (inp <> 'N') AND (inp <> 'n')
    then if NOT (fileexists(libfilename))
        then displayln('There is no library on disk',3,7)
        else begin
            displayln('Loading begins ...',4,2);
            reset(textfile);
            read(textfile,inp);
            while (inp <> '#') AND (library.nrofentries< maxentries) DO
                begin
                    tempentry.key:=inp;
                    read(textfile,inp,inp);
                    tempentry.description:='';
                    i:=1;
                    while inp <> ' ' DO
                        begin
                            tempentry.description:=tempentry.description+inp;
                            read(textfile,inp);
                            i:=i+1
                        end;
                    while i <= (maxdescription +1) DO
                        begin
                            read(textfile,inp);
                            i:=i+1
                        end;
                    tempentry.subdivision:=inp;
                    if eoln(textfile)
                    then begin
                        tempentry.prompt:=FALSE;
                        readln(textfile)
                    end
                    else begin
                        tempentry.prompt:=TRUE;
                        readln(textfile,inp,tempentry.promptinfo)
                    end;
                    library.entries[tempentry.key]:=tempentry;
                    library.nrofentries:=library.nrofentries +1;

```

```

        read(textfile,inp)
    end;
    if (library.nrofentries = maxentries) AND (inp <> '#')
    then REPEAT
        readln(textfile,inp)
        UNTIL inp = '#';
    readln(textfile);
    while (NOT eof(textfile)) DO
        begin
            read(textfile,tempsubddetails.sd,inp,
                tempsubddetails.extrasubd,inp,recordingmode);
        CASE recordingmode OF
            'c': begin
                tempsubddetails.modeofrecording:=continuous;
                readln(textfile)
            end;
            't': begin
                tempsubddetails.modeofrecording:=timesampling;
                REPEAT
                    read(textfile,inp)
                    UNTIL inp = ' ';
                readln(textfile,tempsubddetails.lengthoftime)
                end
            END;
            library.obsdetails[tempsubddetails.sd]:=tempsubddetails
        end;
        close(textfile);
        displayln('... loading ends.',20,4);
        displayln('A library is now loaded in memory',2,6);
        if library.nrofentries = maxentries
        then displayln('Library is FULL',5,7)
        end;
        Delay(3000)
    end; {load}

```

{-----}

```

PROCEDURE addanentry (var library:librarytype);
( ----- )

```

```

var
    inp: char;

begin
    clrscr;
    if library.nrofentries = maxentries
    then displayln('Library is full - no more entries added',1,3)
    else begin
        displayln('Which library subdivision will this',3,1);
        displayln('entry belong to (1-4)? ... RETURN',1,2);
        displayln('Enter 1 if the lib. is NOT SUBDIVIDED',2,3);
        getafterRETURNandcheckentry(35,2,inp,'1','4',1,8);
        makeanentry(library,inp);
        clrscr;
        if inp <> '4'
        then if library.obsdetails[inp].sd = '*'
            then begin
                library.obsdetails[inp].sd:=inp;
                displayln('This s/d has not been used before.',3,2);
                displayln('Enter T or C for the mode of recording',
                    1,3);
                entermodeofrecording(library.obsdetails[inp],inp);
            end
        end
    end
end

```

```

        if nrofsubdivisions(library) < 2
        then library.obsdetails[inp].extrasubd:=
                                                    defaultextrasubd
        else begin
            displayln
            ('Enter the extra s/d for simultaneously',1,5);
            displayln
            ('recorded info or 0 if NONE -- RETURN',1,6);
            writeln('          ',inp,' --');
            checkandenterextrasubd(library,inp);
            clrscr;
            displayln
            ('Do you wish to update the extra s/d s',1,2);
            waitforyorn(40,2,inp);
            if (inp = 'Y') OR (inp = 'y')
            then allocateextrasubds(library)
        end
    end
end;
Delay(3000)
end; {addanentry}

{-----}

PROCEDURE deleteanentry (var library: librarytype);
{ ----- }

var inp,entryid,keyid,endofsearch,exsubd,i: char;
    s: ( searching, found, exhausted );
    sdid: subdivisiontype;

begin
    clrscr;
    displayln('Enter the key of the',3,2);
    displayln('entry you wish too delete -- RETURN',1,3);
    getafterRETURNandcheckentry(38,3,inp,firstentry,lastentry,1,8);
    if library.entries[inp].key = '*'
    then displayln('There is no such entry to delete',1,5)
    else begin
        entryid:=inp;
        displayoneentry(library.entries[entryid],5);
        displayln('Delete this entry? Y/N',1,7);
        waitforyorn(25,7,inp);
        if (inp = 'Y') OR (inp = 'y')
        then begin
            sdid:=library.entries[entryid].subdivision;
            library.entries[entryid].key:='*'; {effective deletion}
            library.nrofentries:=library.nrofentries -1;
            s:=searching;
            keyid:=firstentry;
            endofsearch:=succ(lastentry);
            REPEAT {search the library to see if this was the only}
                if keyid = endofsearch {entry in that s/d}
                then s:=exhausted
                else if (library.entries[keyid].key = '*') OR
                    ((library.entries[keyid].key <> '*')
                     AND (library.entries[keyid].subdivision<>sdid))
                then keyid:=succ(keyid)
                else s:=found
            UNTIL s <> searching;
            if s = exhausted {ie if it was the only entry}

```

```

        then begin
            library.obsdetails[sdid].sd:= '1';
            FOR i:= '1' TO '3' DO
                if library.obsdetails[i].extrasubd = sdid
                then library.obsdetails[i].extrasubd:=
                    defaultextrasubd
            end;
            displayln('Deletion MADE',5,8)
        end
    end;
    Delay(3000)
end; {deleteanentry}

{-----}

PROCEDURE amend (var library:librarytype);
{ ----- }

    var inp,i:char;
        count:byte;

    begin
        ClrScr;
        if library.nrofentries = 0
        then displayln('There is no library to be amended',2,4)
        else begin
            REPEAT
                ClrScr;
                displayln('AMEND MENU',12,1);
                displayln('(1) ADD an entry',4,2);
                displayln('(2) DELETE an entry',4,3);
                displayln('(3) CHANGE MODES of recording',4,4);
                displayln('(4) CHANGE EXTRA subdivisions',4,5);
                displayln('(0) QUIT & return to library menu',4,6);
                displayln('CHOICE ...',12,7);
                getandcheckentry(24,7,inp,'0','4',2,8);
            CASE inp OF
                '1': addanentry(library);
                '2': deleteanentry(library);
                '3': begin
                    allocatemodeofrecording(library);
                    initializeextrasubdto default(library.obsdetails);
                    if nrofsubdivisions(library) > 1
                    then begin
                        displayln('Also reallocate the extra s/d s for',
                            1,5);

                        displayln
                            ('simultaneously recorded information ...',1,6);
                        Delay(2000);
                        allocateextrasubds(library)
                    end
                end;
                '4': if nrofsubdivisions(library) > 1
                    then allocateextrasubds(library)
                    else begin
                        ClrScr;
                        displayln('The library is not subdivided so',3,2);
                        displayln('there is no opportunity to use',1,3);
                        displayln('extra subdivisions.',1,4);
                        Delay(2000)
                    end
            end
        end
    end
END

```

```

        UNTIL inp = '0';
        ClrScr;
        displayln('Do you wish to store the amended',3,2);
        displayln('library on disk',1,3);
        waitforyorn(18,3,inp);
        if (inp = 'Y') OR (inp = 'y')
            then storelibrary(library)
        end;
        Delay(3000)
    end; {amend}

{-----}

PROCEDURE librarymenu (var library: librarytype);
{ ----- }

    var choice: char;

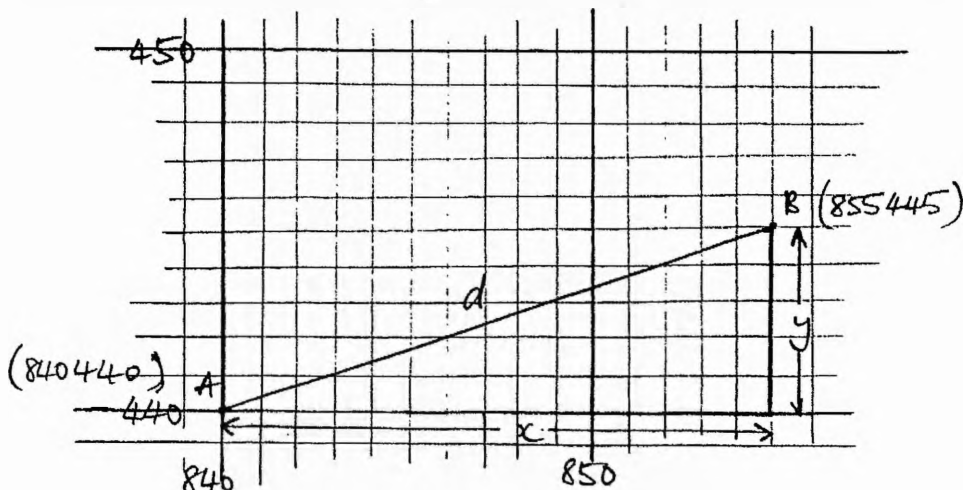
    begin
        initializelibrary(library);
        REPEAT
            ClrScr;
            displayln('LIBRARY MENU',12,1);
            displayln('(1) Create a new library',6,2);
            displayln('(2) Load in a previous library',6,3);
            displayln('(3) Amend current library',6,4);
            displayln('(4) Display current library',6,5);
            displayln('(0) Quit and return to main menu',6,6);
            displayln('CHOICE ... ',12,7);
            getandcheckentry(24,7,choice,'0','4',2,8);
            CASE choice OF
                '1': create(library);
                '2': load(library);
                '3': amend(library);
                '4': display(library)
            END
        UNTIL choice = '0';
        ClrScr;
        displayln('*** End of Library Session ***',5,4);
        Delay(3000)
    end; {librarymenu}

BEGIN {main program}
    ClrScr;
    displayln('LIBRARY FOR MBUNI PROGRAM',1,3);
    displayln('Press any key to continue ...',4,6);
    waitandgetchar(35,6,junk);
    librarymenu(library);
    ClrScr;
    displayln('*** End of program ***',4,3)
END.

{*****}

```

ALGORITHM FOR CALCULATING DISTANCES FROM 6-FIGURE GRID REFERENCES.



In order to calculate distance d between locations A and B, we need to compute distances x and y . Then using Pythagorus' equation, $d^2 = x^2 + y^2$.

In 6-figure grid references, the first 3 digits refer to the location of the point in a West-East direction (W), and the second 3 digits refer to the location in a South-North direction (S). (The first two digits represent the main grid squares, and the third digit represents tenths of this larger unit, e.g. tenths of a kilometer). Therefore,

$$\text{location A} = W_A S_A \quad \text{and} \quad \text{location B} = W_B S_B$$

" $m \text{ DIV } n$ " is an operation which divides m by n , producing only the whole number part as the result.

$A \text{ DIV } 1000 = W_A$ (i.e. the first 3 digits of a 6-figure grid reference)

$$\text{e.g. } 840440 \text{ DIV } 1000 = 840$$

" $m \text{ MOD } n$ " is an operation which divides m by n , producing only the remainder as the result.

$A \text{ MOD } 1000 = S_A$ (i.e. the second 3 digits of a 6-figure grid reference)

$$\text{e.g. } 840440 \text{ MOD } 1000 = 440.$$

$$x = W_B - W_A \quad \text{and} \quad y = S_B - S_A$$

$$\text{Therefore, } x = (B \text{ DIV } 1000) - (A \text{ DIV } 1000)$$

$$\text{and } y = (B \text{ MOD } 1000) - (A \text{ MOD } 1000)$$

The results of these calculations could be negative if distance travelled is not W -> E and S -> N. Taking the ABSOLUTE value (ABS) means that only the magnitude of these values is considered, and that the sign is ignored.

Therefore, $x = \text{ABS} ((B \text{ DIV } 1000) - (A \text{ DIV } 1000))$

and $y = \text{ABS} ((B \text{ MOD } 1000) - (A \text{ MOD } 1000))$

Using Pythagoras' equation, $d = \sqrt{x^2 + y^2}$
i.e. $d = \sqrt{\text{SQR}(x) + \text{SQR}(y)}$

where x and y are as above.

Example:

A = 840440 B = 850445

$x = (850445 \text{ DIV } 1000) - (840440 \text{ DIV } 1000)$
 $= 850 - 840$
 $= 10$

$y = (850445 \text{ MOD } 1000) - (840440 \text{ MOD } 1000)$
 $= 445 - 440$
 $= 5$

$d = \sqrt{\text{SQR}(x) + \text{SQR}(y)}$
 $= \sqrt{10^2 + 5^2}$
 $= \sqrt{125}$
 $= \underline{11.2}$

The distance between locations A and B is therefore 11.2 of the smallest unit of distance i.e. 11.2 tenths of a kilometer, in this example, = 1.12km.

APPENDIX C

USERS' GUIDE TO 'MBUNI'

**'MBUNI':
A COMPUTER PROGRAM TO RECORD FOCAL ANIMAL
BEHAVIOUR.**

USERS' GUIDE

Version 1.2

© Frances Marsh

SCOTTISH PRIMATE RESEARCH GROUP
Psychological Laboratory,
University of St. Andrews,
St. Andrews,
FIFE, SCOTLAND.

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I BEFORE THE PROGRAM

This document is not only a manual of instructions for the program 'MBUNI', but a guide to using this particular tool in computerised collection of behavioural data. The following parts of this section therefore provide a background to using computers to record data, and introduce the features of 'MBUNI' in particular, as a basis for actually running the program which is then described in detail in section II. To complete the information, the third section then deals briefly with the results produced by using 'MBUNI'.

1. Background

Since the 1950s, the advantages of collecting behavioural data by computer have been recognised. Early computerised methods of recording behavioural data have involved specially constructed but cumbersome devices or specially written programs. These could often only be used for the project for which they were designed, meaning that isolated establishments would each be employing their own method of data collection. Problems of machine portability meant that on the whole behavioural researchers, and fieldworkers in particular, have been reluctant to abandon the old pencil-and-paper method of using check sheets, even though this results in hours of transcribing the data into a computer for analysis.

In the last decade, two notable improvements have been the set of programs called ETHOGRAM developed by Kevin Browne to be run on an Epson portable machine, and the programs written by Barton and Whiten to collect focal animal data on a Hewlett-Packard hand held computer. Both these programs meant data could be successfully collected in the field, but due to their being written in BASIC languages they are machine dependent, which is a limitation at a time when continual improvement of hardware means machines are quickly made redundant and the software has to be rewritten.

With the advent of smaller and readily available portable computers which could easily be used for recording behavioural data by direct observation, opening up the area of non-laboratory environments to computerisation, there has been a need for a data collecting program flexible enough to be of use to any researcher interested in behaviour. This was therefore the idea behind the development of this program.

My own aims of collecting baboon behavioural data in the field in Kenya and my training in computer programming has resulted in 'MBUNI', a program for focal observations. Written in Pascal, this program can be run on any IBM compatible

machine which uses the now universal MS-DOS. 'MBUNI' can be used to collect data on behaviour for any project particularly in non-laboratory settings where portability and ease of use are important, storing the data in a form which can then be easily used in conjunction with the many manipulative packages and databases now available.

'MBUNI' was developed and tested during 11 months in the field using a DIP/Atari 'Portfolio' pocket computer (Figure 1).

2. Introduction to the features of 'MBUNI'

All that is needed to use 'MBUNI' is a computer with at least one disk drive (minor alterations are necessary if it is to be run on a computer with a hard disk), and a well designed project. I cannot stress enough that 'MBUNI' is just a tool (like your pencil and paper) and for the data it records to mean anything, you, the user, must be clear about what it is you want to collect, and how the data will answer the questions your research is asking. Well defined and designed behavioural categories are essential.

The program is menu driven and has clear error messages, so should be easy to follow and use.

2.1 Data collection.

'MBUNI' uses the principle of having key presses represent the occurrence of defined behaviours. The user creates a 'library' of behaviours that are to be associated with specified keys, and decides upon certain features to do with how the data are recorded, and all this information is stored in the library. This library is then loaded in before doing a focal session and automatically consulted during the 'Observation' part of the program. When a key is depressed the time and date are automatically recorded (if behaviour is being recorded continuously), and consecutive key presses enable durations of the associated behaviour to be calculated during analysis of the data. Different 'libraries' can be set up for different projects and then just be loaded in for different focal observation sessions.

2.2 Continuous vs. time sampling recording.

Although one of the particular advantages of using a computer to record data is the ability to collect data continuously, you may prefer to use a time sampling method. The user defines which method of data collection he wishes to use and this information

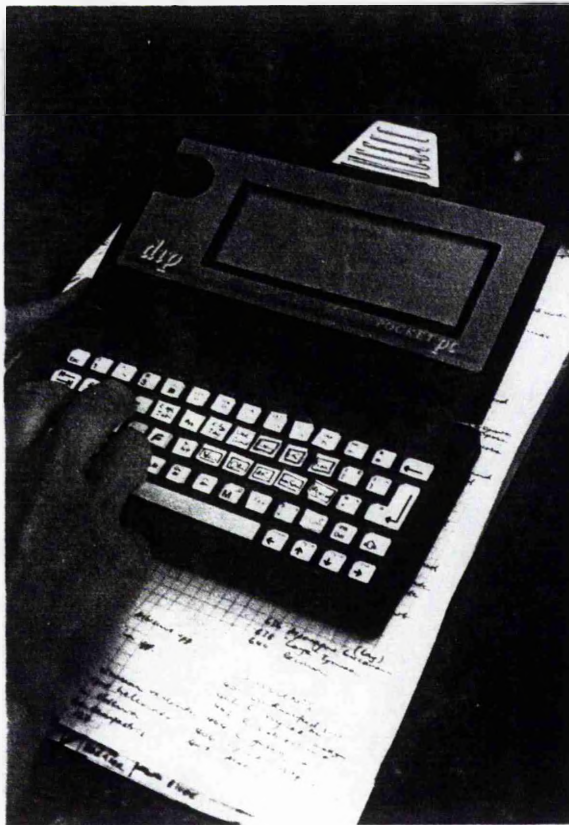


Figure 1: DIP 'Portfolio' being used in the field.

is stored in the 'library'. If a method of time sampling is preferred, then during 'Observation', the user presses a key to denote the behaviour occurring at the instant of the timer's bleep.

2.3 Subdivisions of the library of behavioural categories.

The library of behaviours can be divided into up to three subdivisions, the behaviours in each subdivision not needing to be mutually exclusive of those in any other subdivision. For example, one subdivision may be made up of behaviours relating to activities of the subject (like walking, eating, talking) and another of behaviours relating to the place of activity. (The number of subdivisions has been limited to three because our experience has been that in practice it is difficult to keep track of more.) Data collected for different subdivisions is stored in separate data files.

The option of subdivisions may not be helpful to all projects, so do **not** feel obliged to subdivide your library of behaviours.

One advantage of having more than one subdivision of the library is that different methods of data collection could be used for each subdivision: one set of behaviours can be recorded continuously and another using a time sample method which at intervals interrupts the continuous recording.

2.4 'Looking into' another subdivision.

'MBUNI' also has the feature of being able to store in a single file the behaviour being recorded for that subdivision and to additionally store automatically whatever is *currently* being recorded for another subdivision. For example, when a subject is recorded as eating, the information of where he is eating, recorded in a different subdivision by an earlier key press, is simultaneously "looked up" and stored in the one data file. However, if this "extra" data in the other subdivision is changed by any further key presses of behaviours in that subdivision, then the simultaneously stored data on file is not updated: the extra data represents the state of another subdivision at the instant of the key press of the primary subdivision i.e. at the initiation of the behaviour in that subdivision. Although this option means a duplication of data storage it can be a useful feature for easily building up an alternative framework of analysis for a subject's behaviour (i.e. having your cake and eating it!). The value of this feature depends entirely on the design of your project. It was used by one worker where the behaviour recorded in the second subdivision was general group activity, something which does not change very rapidly, and which could relevantly be looked at as an instantaneous

snap-shot from within another subdivision. However, for rapidly changing behaviour, there would be great and inappropriate loss of meaning in these data. Hence this feature may not be useful to every worker, and so again do not feel obliged to use it if you do not think it will enhance your data. (See also diagram and explanation in section II.)

2.5 A fourth subdivision to use as a shorthand notation.

It is also possible to have a fourth subdivision of the library which is made up of entries specifically reserved to be used only as a shorthand for frequently used or cumbersome information that would otherwise have to be entered in full during the observation procedure, e.g. food codes. These entries will not be usable as behaviours in either continuous or time sample recordings during 'Observation'.

In section II, the means of creating a library of behaviours, the procedure for carrying out observations using the library, and the process of data recording are described in detail.

3. DIP/Atari 'Portfolio'

Although it is not intended that this manual should include information on the operation of the DIP/Atari 'Portfolio' as such, I will include some notes on how to configure the computer so that 'MBUNI' can be run. These instructions should be followed to set up the computer initially and after every battery failure etc.

1. Use the command FDISK 8 <rtm> to make the disk space in Drive C as small as possible, so as to leave as much internal memory space as possible for running 'MBUNI'.

2. Make a CONFIG.SYS file (as suggested in the 'Portfolio' manual) on Drive C which will be used by the machine every time it is re-booted with CTRL-ALT-DEL. Include in it the lines:

```
FILES=20  
COUNTRY=044
```

But do not include anything on BUFFERS as setting this takes up too much room in the memory. (A copy of the CONFIG.SYS file can be stored on a memory card and copied onto Drive C when necessary.)

3. After re-booting the system, use the SETUP option in the 'Portfolio' to set the DISPLAY so that the computer will act like a static PC and not scroll the screen up.

ie.: SETUP- DISPLAY- EXTERNAL MODE- STATIC.

All these things should be checked prior to running the program (and if you find things are not going as you think they should). After re-booting and checking these details, also check that the internal TIME and DATE are correct as these are also lost and set to an incorrect default value after battery failure.

II USING THE PROGRAM

Because of the limited size of the memory which can be used when running 'MBUNI', I have now made the creation of the 'library' part a separate program and just left the procedures for loading in and displaying a library in 'MBUNI' proper. The first program then is 'MB_LIBRARY.EXE' and this should be used to create the library and make all the necessary definitions of how data should be collected. Then, 'MBUNI.EXE' is run to use this library and record the observations.

1. Mb_library

This program is run by typing 'mb_library' (including in the command the disk drive where the program is located if necessary) and pressing <return>. It can be run on any IBM compatible machine including normal desktop PCs (and on a Mackintosh if it is running the suitable software to make it emulate an IBM PC ???), or on the 'Portfolio' itself, though this is somewhat more awkward because of the small keyboard (and because at the moment the screen presentation is shifted one character to the right and so the edge might be lost).

On starting the program, the user is presented with the **LIBRARY MENU**. This presents the user with five choices (described below) which can be used to generate a library of behaviours, associating keys with behavioural categories and making decisions about the method of data collection, to be then used in the observation process. Figure 2 is an example of a library which has been used to collect data. The library is stored in a file called 'library.txt' on **Drive A**.

1.1 Create a new library.

When using 'MBUNI' for the first time, a library will have to be created (although once created that library can then be read in again from disk). **N.B.** if a new library is to be created and one already exists on the disk in Drive A, it will overwrite that one in memory and on disk. **Make sure there is a disk in Drive A: otherwise the program will crash when it comes to store the library at the end of creating it!**

1.1.1 Making the basic entries.

Any number of keys and associated behaviours can be entered into the library, up to a maximum of 70. Legal keys that can be used are : 'A' - 'Z', 'a' - 'z', '0' - '9', ',', '<', '.', '>', ';', ':', '/', '?'. .

For each entry, the user is asked for the **KEY** to identify and associate with the following behaviour details - enter a key and then press <return>. If the key entry is not a permissible entry or there is already an entry for that key, then an error message appears and a replacement must be made.

The user is then asked for the **DESCRIPTION** of the behaviour to be associated with the key (less than 18 characters in length) - enter that and then press <return>. Next it asks whether on the depression of that key, there should be any **PROMPT** for further information - [Y/N]. Obviously, if the entry key is to be shorthand for a frequently used or long description (subdivision 4) then **NO** prompted information should be requested. If **PROMPTED INFORMATION** is required, then the user should enter what the prompt should be (less than 15 characters) and press <return>. For example see entries in Figure 2.

After each entry is completed you are asked if you want to **RECORD** this entry - [Y/N] - ('N' if you have made a mistake and wish to cancel this entry), and whether you have **FINISHED** making the library - [Y/N] - ('N' if more entries are to be added).

1.1.2 Subdividing the library.

The user is then asked:

Do you wish to sub-divide the library? [Y/N]

The idea of having data recorded in separate subdivisions is illustrated in Figure 3. Using the keys from the library in Figure 2, this shows how **three** kinds of data can be collected in parallel, but stored in separate files.

If the response is 'N', then the whole library will be treated as subdivision '1'. If the response is 'Y' then there follows two screens of information describing what is possible, and how to continue.

Each key entry in the library plus its details is presented on the screen and the user has to allocate the entry to a subdivision (1-4) and then press <return>. N.B. Subdivision 4 is only for key entries which are going to be used as a shorthand. This continues until all the entries have been allocated a subdivision to belong to. (See

Figure 2: Example library used by 'MBUNI'. The chosen keys are listed alphabetically, with the behavioural categories they represent, the subdivision they belong to, and the prompts which appear on the screen when certain keys are pressed. At the bottom is the stored information about each defined subdivision, the subdivision it 'looks into', and its mode of recording.

key	behaviour	s/d	prompt
,	rejection	1	
/	out_of_sight	1	
0	997.00	4	
1	999.99	4	
2	901.06	4	
3	101.06	4	
4	512.00	4	
5	600.13	4	
6	618.02	4	
7	105.13	4	
8	105.22	4	
9	616.01	4	
;	beyond_5m	3	
G	nipple_position	1	
Q	being_groomed	1	by whom?
R	receiv_affil_appr.	1	
U	male_in_conflict	1	which male?
W	supplanting	1	
Y	receiv_aggression	1	
a	resting	1	
b	attd_environ.	1	
c	social_expl	1	
d	expl_for_food	1	
f	feeding	1	on what?
g	on_nipple	1	
h	ventral_contact	3	
i	within_1m	2	which male?
j	other_contact	3	
k	within_arms'_reach	3	
l	arms'_reach_->_5m	3	
n	attd_social	1	
o	1_to_5m	2	which male?
p	no_male_within_5m	2	
q	grooming	1	whom?
r	make_affil_appr.	1	
s	moving	1	
t	avoid	1	
u	carried_by_male	1	which male?
v	vis_attd_(indist)	1	
w	supplanted	1	
x	environ_expl	1	
y	aggress	1	
z	active_expl	1	
#			
1	2	continuous	
2	3	continuous	
3	0	continuous	

Figure 2 for examples.)

1.1.3 Continuous vs. time sampling recording.

The user is next asked to **indicate the modes of recording for each subdivision created**. (This screen flashes up rather quickly, but it will pause when it requires information from you.) The user is asked to enter **T** or **C** for each subdivision as presented on the screen (without needing to press <return>). If the library is not subdivided then it is being referred to as subdivision '1' and so a response should be made for that subdivision.

The tone of the bleep which is used during the program and any time sampling is constant, so it is advised that only **ONE** subdivision is used for time sampling: if multiple subdivisions use time sampling, it would be difficult to differentiate between them.

If **T** is chosen for a subdivision, then the user is asked to enter the duration of the **TIME INTERVAL** between bleeps. This should be entered in **SECONDS**. At present this does not appear on the screen but it is read in to the computer, so just complete the entry by pressing <return>.

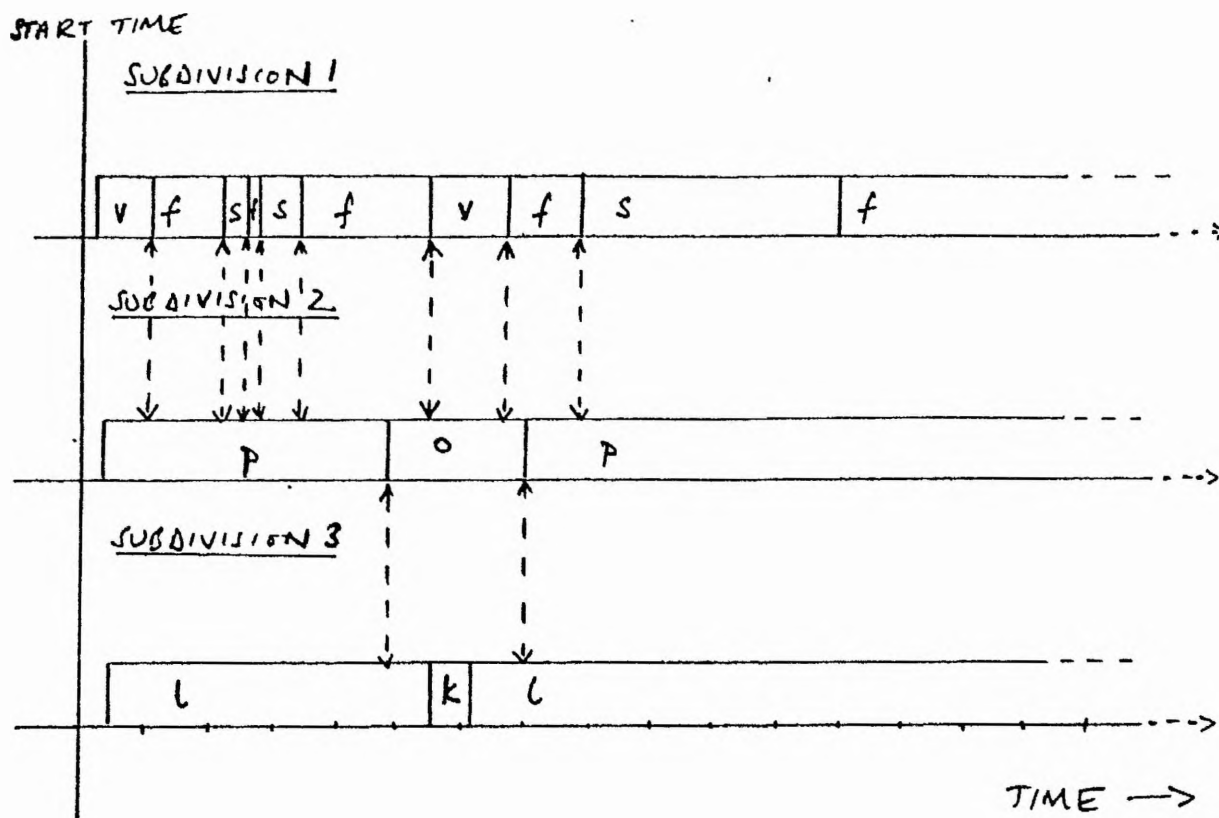
1.1.4 Simultaneous recording from two subdivisions.

The user is asked if he wants to use this feature of 'MBUNI': **Do you want to record information simultaneously for two subdivisions? - [Y/N]**. This feature is illustrated in Figure 3. Whenever a key is pressed to record data in the primary subdivision, the computer simultaneously records what it has currently stored in the secondary subdivision. N.B. the problems of this information not being updated, have been discussed earlier (I.2.4).

Enter the **primary subdivision** first and then <return>, and then the **secondary subdivision from which the 'extra' information should come**, followed by <return>. '0' followed by <return> then finishes this section.

A library is now in memory and a copy automatically made on disk in the file called 'library.txt' on Drive A - **make sure there is a disk in Drive A!**

Figure 3: Illustration of data collection using more than one subdivision, and using the example library from Figure 2. Data in subdivisions 1 - 3 are recorded in parallel continuously by depressing keys on the keyboard, with the data from each subdivision being stored separately.



N.B. The library in Figure 2 is set up for subdivision 1 to 'look into' subdivision 2, and subdivision 2 to 'look into' subdivision 3. So when a key in subdivision 1 is pressed, whatever is being currently recorded in subdivision 2 is recorded as 'extra' data, and similarly for subdivision 2 and 3 (<----->)

1.2 Load in a previous library.

If you have used 'MBUNI' before and created a library which is stored on disk, you can **LOAD** this library from disk into memory to save creating the same library again. N.B. A disk with a library on it must be in the disk drive when loading, or the program will crash. Amendment of this loaded-in library can be made using the 'Amend' choices if small changes to substantially the same library are required. If a library already exists in memory it will be overwritten if you chose to continue after the warning message.

A library is now in memory.

1.3 Display the current library.

This choice enables you to view the information existing in the library which is currently in memory (the entries and the details which will be referred to during observation), after having used the creation, loading or amending processes. The two types of library information can be seen by selecting the appropriate option:

- (1) Display library entries
- (2) Display details about the subdivision used during observation.
- (0) Quit.

(1): Entries in the library are displayed on the screen in the form

Key	Description	Subdivision	Prompt
-----	-------------	-------------	--------

The user is prompted to press any key to continue the display so that it can be viewed at his own leisure, and is informed of the end of the library.

(2): Details of subdivisions to be used during observation which are stored in the library are displayed in the form

Sub/d	Extra sub/d	Mode of recording	Length of time
-------	-------------	-------------------	----------------

Only information for the subdivisions that exist is displayed. The user is prompted to finish the display by pressing any key.

1.4 Amend the current library.

Amending the library in memory involves using components of 'Create a new library', detailed in section II.1.1. In order to change entries in the library, follow the menus, and refer to the information in II.1.1 where necessary.

1.5 Quit and return to Main Menu.

After obtaining a copy of a library of behaviours in memory and on the disk in Drive A by creating/ loading/ amending, leave 'MB_LIBRARY', and next use 'MBUNI' in order to record observational data.

2. 'Mbuni'

The program is run by typing 'mbuni' and pressing <return> (including the drive being used). Initially when entering the program you are presented with a choice of the two parts of the program:

- (1) Library
- (2) Observation or Quit the program.

(Ignore the LOCATION section if it is included, as this is specifically to calculate and record distances using 6-figure grid references.)

A library of behaviours must exist in the computer's memory before observations can be made (since the library entries and the associated information are used during observations). If the choice of (2) OBSERVATION is made without there being a library, an error statement appears.

2.1 Library.

When first using 'MBUNI' in any session, chose (1) LIBRARY and **LOAD** in a library to be used in that session (see II.1.2). If another observation period is required having been using the program already, just select (2) OBSERVATION as the library will remain in memory.

2.2 Observation.

Make the choice (2) from the main menu.

2.2.1 Starting the session.

Before starting to make observations, the user is asked for the **FILE NAME** (no more than 6 characters) for where the data will be stored on the disk in Drive A. The file name will always be suffixed by the subdivision number, since the data recorded for different subdivisions is stored in separate files.

Then the user is asked for the identity (**ID**) of the focal subject whose data is going to be recorded. This must be 3 or less characters (i.e. a code) - any more characters will be ignored.

The screen is then set up for making observations. The top line of the screen displays the identity of the focal subject, the current time, which is updated after each key press or every minute (whichever is sooner), and the key which has just been pressed. Then the screen is divided up to present visually the information currently being stored for each subdivision of the library, the portion of the screen available depending on the number of subdivisions existing (e.g. if the library is divided into 2 subdivisions, half the screen is available for displaying what is stored for each subdivision). If the library of behaviours is undivided, it is treated as a single subdivision 1.

The user is asked to **press any key to start ...**, so that he can locate his focal animal and be sure he is ready. After pressing a key, the user must then wait till the computer has counted up to the next **whole minute** and then a **bleep** indicates that it is time to start the focal session.

2.2.2 Doing the focal observation.

During observation, occurrences of behaviours (those entered in the current library) are recorded by the depression of the appropriate keys on the keyboard. Data entries made by pressing keys are displayed on the screen, with the description as stored in the library.

An observation session lasts **30 minutes** and is ended **automatically**, signified by a **double bleep sound**. If it is necessary to end the observation period any earlier, this can be done by holding down the **CTRL** key and pressing the key '**S**'. This cuts short the session immediately, but makes no provision for the normal neat completion of the session or for rejoining it at all later and so should only be used in an emergency.

If data is being recorded continuously for the behaviours in a subdivision, the data entries are key driven i.e. there is no prompting of the user for data: the depression

of a key initiates the recording process, and any key for which data is being recorded continuously (i.e. in a subdivision allocated as being for continuous recording) can be pressed at any time to make a data entry. If data is being recorded using a time sample method for the behaviours in a subdivision, the data entries are time driven i.e. at the prompt of a single bleep the user must press a key which belongs to that subdivision for which the timer has gone off - any other key will result in an error statement appearing and a replacement entry must be made. Entries can be made into a time sample subdivision at any time though, so be sure to wait for the bleep before making the data entry for that subdivision.

At the start of the observation session therefore, the screen below the top line is blank apart from an indication of the parts of the screen dedicated to displaying information about the subdivisions that exist. For each subdivision a data file is created and initialised with the starting time of the session. A timer is started for each subdivision which has been designated as using time sampling for its method of recording, which continually checks the time to see if the appropriate length of time between sampling instants has passed yet. Data entries can therefore be made by the depression of keys (at any time) for behaviours that are being recorded continuously, and when it is time to make an entry for the behaviours being recorded using time sampling, the computer beeps to prompt the user to make a key press.

At the press of a key, from a continuous or timesampling subdivision, the description of the behaviour associated with the key in the library of behaviours is displayed on the screen in the appropriate portion of the screen for that subdivision. If for that key there should be a prompt for more information, then the behaviour description is followed on the screen by the appropriate prompt being displayed. For example for the key press associated with eating, the user may have decided to have a prompt of 'what food?' for further information. The user MUST enter something, either the appropriate information or a '?', and then press <return>. It is here that the keys in subdivision '4' which represent lengthy descriptions as a shorthand single key can be used. If a single key is entered as prompted information followed by <return>, the entry is checked for existence as a shorthand in the library. If it exists, the longhand description is displayed and stored as prompted information. (A little care is therefore needed when making single letter entries. It is advised that no single letter entries are made unless they are a shorthand key.) The computer will wait until <return> has been pressed before proceeding, so any great delay in response to the prompt will cause inaccuracy in any behaviour recording for which real time is important. The response to the prompt in a currently recorded entry can be changed once the entry has been made if you realise a mistake has been made, or you now know what the correct response is in place of the '?' (see below).

When initially made, entries are stored in memory, until another entry is made with a behaviour in the same subdivision or the end of the session is reached. At that point the data entry is then written to the appropriate file on disk for the subdivision that the behaviour belongs to.

This process of entering observed behavioural data continues in this way until the session ends. Each key press is checked for correctness (i.e. its validity as a potential key to be used and its existence in the library as a key with an associated behaviour) and an error message is displayed if an incorrect key is pressed.

Error correction: One other kind of key press can be made at the keyboard during an observation session, which does not initiate the process of making a data entry as described above, but which can be used to affect the records of behaviours currently being held in memory. The user can at any time after an entry has been completed press the 'ESC' key to **alter what is currently being recorded** for any of the subdivisions that exist.

After depressing the **ESC** key, you are prompted for which **subdivision** of those that exist and are used during the observations you wish to affect. The choice is then to enter CTRL-E to mark a current observation entry in that subdivision as being an error; CTRL-P to alter the prompted information currently stored for the entry of that subdivision; or ESC to <return> to the observation process. Again the machine waits for a response and so speed of reply means greater accuracy for observations where time is important.

If **CTRL-E** is entered, the current observation in that subdivision is stored on disk with '****' instead of the focal identity code preceding the entry. The user is asked to enter an alternative key for a corrective entry or '**ESC**' if no such entry is desired. The error flagged data entries can then easily be located and deleted from the data file after the session.

If **CTRL-P** is entered, the current prompted information entry is removed from the screen display and the user should then enter an alternative, and then press <return> to make the entry.

On completion of any alterations you are then automatically returned to the observation process, ready to make another entry by a key press and have any time sampling timers checked.

2.2.3 Ending the session.

An observation session is ended automatically, and indicated by a **double bleep**. You are then returned to the main menu of the program with the choice to do another observation with the same library, load in a different one, or quit from 'MBUNI'.

III AFTER THE PROGRAM: DATA STORAGE AND MANIPULATION.

Data collected by using 'MBUNI' is stored on a disk in **Drive A** of the computer. While still running the program, even when having completed an observation session and returned to the main menu, it is NOT possible to look at the data collected. You must QUIT from the main menu and be returned to the MS-DOS prompt and then use MS-DOS commands to look at the files stored on disk.

Two kinds of data are stored on disk: LIBRARY data in a file called **library.txt**, and OBSERVATION data in up to three separate files, one for each subdivision of the library of behaviours that you made and then used during the observation process. These are named **xxxxxx_1.txt**, **xxxxxx_2.txt** etc..

Data in all these files is stored rigorously in columns and so is suitable to be read into a database, or to be used with statistical packages such as SPSSx. Manipulation and analysis is then straightforward to carry out. (I have successfully used SPSSPC for analysing the data I collected).

Data entries recorded continuously are stored in the form:

FOCAL ID. KEY PRESSED PROMPTED INFORMATION TIME DATE

Entries recorded using time sampling omit the time and date.

In addition to these data, if the subdivision of the behaviour associated with the key pressed is one where information on what is currently being recorded at that moment in another subdivision is to be recorded (see I.2.4 and II.1.1.4), then there will also be data on the EXTRA KEY and EXTRA PROMPTED INFORMATION recorded following that shown above.

Figure 4 is an example of the recorded data for one subdivision.

N.B. Library data is necessary in addition to the observation data not only for using during the observation process for use by the computer, but also to provide information on the behaviour that is represented by the key presses recorded in the observation data files. TOGETHER the two kinds of data form an integrated set: different libraries may use different keys associated with different behaviours and so the data from the particular library used to make the observational recordings MUST be kept with them.

Figure 4: Extract from example of data collected using 'MBUNI' and the library in Figure 2. Columns store the ID of the focal animal (kk), the key pressed (e.g. f = feeding), the prompted information (e.g. 101.06 [food code]), time, date, and 'extra' information (key and prompted information currently being recorded from the subdivision being 'looked into') (e.g. p -).

***		9:52:00	25:10:1990		{start time}
kk	v -	9:52:01	25:10:1990	- -	
kk	f 101.06	9:52:12	25:10:1990	p -	
kk	s -	9:52:20	25:10:1990	p -	
kk	f 999.99	9:52:32	25:10:1990	p -	
kk	s -	9:52:34	25:10:1990	p -	
kk	f 556.99	9:52:41	25:10:1990	p -	
kk	v -	9:53:03	25:10:1990	p -	
kk	f 111.06	9:53:38	25:10:1990	p -	
kk	, -	9:54:05	25:10:1990	p -	
kk	s -	9:54:08	25:10:1990	p -	
kk	v -	9:54:10	25:10:1990	p -	
kk	s -	9:55:53	25:10:1990	p -	
kk	G -	9:55:54	25:10:1990	p -	
kk	s -	9:56:12	25:10:1990	p -	
kk	v -	9:56:14	25:10:1990	p -	
kk	s -	9:57:37	25:10:1990	p -	
kk	f 999.99	9:57:42	25:10:1990	p -	
kk	s -	9:57:45	25:10:1990	p -	
kk	v -	9:57:47	25:10:1990	p -	
kk	s -	9:59:01	25:10:1990	p -	
kk	f 999.99	9:59:07	25:10:1990	p -	
kk	s -	9:59:13	25:10:1990	p -	
kk	v -	9:59:16	25:10:1990	p -	
kk	s -	9:59:48	25:10:1990	p -	
kk	d -	9:59:50	25:10:1990	p -	
kk	g -	9:59:53	25:10:1990	p -	
kk	v -	10:00:18	25:10:1990	p -	
kk	s -	10:01:58	25:10:1990	p -	
kk	d -	10:02:04	25:10:1990	p -	
kk	f 901.06	10:02:05	25:10:1990	p -	
kk	f 999.99	10:02:17	25:10:1990	p -	
kk	f 101.06	10:02:21	25:10:1990	p -	
kk	s -	10:02:32	25:10:1990	p -	
kk	f 101.06	10:02:39	25:10:1990	p -	
kk	v -	10:02:43	25:10:1990	p -	
kk	s -	10:04:58	25:10:1990	p -	
kk	f 101.06	10:05:02	25:10:1990	p -	
kk	s -	10:05:07	25:10:1990	p -	
kk	f 903.06	10:05:16	25:10:1990	p -	
kk	f 902.06	10:05:45	25:10:1990	p -	
kk	s -	10:05:49	25:10:1990	p -	
kk	d -	10:06:34	25:10:1990	o hx	
kk	s -	10:06:37	25:10:1990	o hx	
..
..
kk	f 997.00	10:21:49	25:10:1990	p -	
...		10:22:00	25:10:1990		{end time}

APPENDIX D

STT PROJECT MANUAL VOLUME II: METHODOLOGY

SOITOITASHE PROJECT MANUAL

VOLUME II : METHODOLOGY

(Volume I: GENERAL is a guide for one's first visit to Chololo
Volume III is the Field Assistant's Manual)

Frances Marsh, Andy Whiten, Robert Barton, Isy Saunders.

SCOTTISH PRIMATE RESEARCH GROUP
Psychological Laboratory,
University of St. Andrews,
St. Andrews,
FIFE, SCOTLAND.

LONG TERM RECORDS: notes on their completion.

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Appendix I: Diagrams and definitions of female reproductive
states; codes for body condition.

Appendix II: Definitions of age-sex categories.

Appendix III: Codes for ad libitum data collection.

Appendix IV: Definitions of habitat types; diagrams of
transects.

Appendix V: Sample record sheets.

INTRODUCTION

The long-term records of the site at Chololo are made up of a variety of separate records, which it is the duty of the students and/or assistants at the site to maintain, in addition to their own special project.

Some records, i.e. of troop census and female reproductive (sexual) states, are completed daily in the field by at least one person who is with a troop. Other records, i.e. life history records, predation summary and inter troop encounters, are completed and updated appropriately from ad libitum field notes at the end of the day.

Most of the information collected on these several sheets is summarised in the monthly demographic record which acts as a complete and important record of the long-term aspects of observing the troops of baboons at Chololo. The records mentioned above are the means by which the monthly summary is achieved, but it is the monthly demographic record itself which is of greatest importance to the long-term records of the project, so every effort should be put into its full and accurate completion. Other records should of course correspond with the summary made and be kept up to date (at least every month).

Additionally, long-term records are kept on the environmental ecology of the study area: i.e. daily climatic records and monthly ecological monitoring. This is a special feature of the site at Chololo (no other site that we know of is collecting such detailed ecological data) and it is vital for the long-term analysis that this side of the long-term data collection should be maintained.

The procedures for these long-term records were set up in the field by Robert Barton in 1986 and derived from those already used by Shirley Strum/UNBP, and by Whiten and Byrne previously in the Drakensberg.

The long-term records are considered to belong to "The Project", which is co-ordinated by A. Whiten. (This is one "pay-off" for the work of supervising individual students' projects.) The plan is thus to publish long-term analyses, with AW directing this and most often likely to be the major author, with other contributors to records as co-authors

(or where circumstances warrant it - e.g. major event in "your year"-major author).

The following sections describe each of the records in detail, with instructions on how to collect the data and complete the sheets. See also the completed sheets for examples of the records (Appendix V).

THE RECORDS

1. Daily data collection

Each day, data on the presence and absence of individual animals and data on the sexual state of all cycling females should be collected. Additionally on a day-to-day basis, ad lib records of affiliative and agonistic behaviour, mating, predation, injuries etc. should be made whenever their occurrence is observed (as is feasible within the scope of one's own focal studies). This information then serves to complete and update the life history, predation and inter-troop records and ultimately the monthly demographic summary, as well as providing information on rank and friendships, and general troop behaviour.

The following sections describe the record sheets which should be carried every day in the field, and those that should be updated on a daily basis.

1.1 DAILY CENSUS (REGISTER):

This is a record of the presence or absence of each of the individual baboons in our troops, and is used to calculate the number of baboons "in" the troop for the monthly demographic summary.

It is probably best to try and complete this record first thing in the morning when first locating the baboons, and then to update any gaps at set periods in one's daily routine (e.g. mid-morning, mid-day, and the end of the day) as is convenient. Strictly, an animal is counted as being 'in' the troop that day if it is observed for any part of the day. (SCS uses the criterion of whether an animal was there for the majority

of the time the troop was being watched for counting an animal as 'in' or 'out' in a day.)

If there is a field assistant working with you, this basic data collection could be part of his daily routine. However, it is IMPORTANT that you are equally competent at censusing the troop for the periods when he is on leave or for when the troop splits and he is no longer in contact with the whole troop. Work on the daily census together.

1.2 REPRODUCTIVE CYCLE STATES:

Each day, a record is made of the condition of each subadult and adult female's paracallosal skin (colour and swelling), one sheet covering each month. This provides information on their reproductive state, the length and pattern of their menstrual cycles, and the length of periods of lactational ammenorhea etc. As well as providing important long-term demographic information, these data can be correlated with ecological data in analyses of the long-term effects of the environment on behaviour.

Details of the codes used and explanatory diagrams are in Appendix I. Each code consists of a two digit number denoting non-swollen or swollen states. For non-swollen states the first digit represents zero swelling (0), menstruation (7), pregnancy (8) or lactational ammenorhea (9); and the second digit represents the colour of the paracallosal skin. For swollen states, numbers 10 - 50 are used as codes for the size of the swelling. There are important distinctions between each of these codes which the diagrams in Appendix I should help explain, but practising in the field until your assessments are compatible with those of other experienced workers is essential. (In the past, more complex gradations of size have been used, but this has mainly been abandoned.) Codes 62 - 68 are used for recording detumescence of the swelling.

The extent of changes of colour in the paracallosal skin varies between individuals and depends on age: after pregnancy where the paracallosal skin becomes very bright pink, young females return to a grey colour, but older females stay mostly pink with a little grey. Experience in the field and practising these assessments is the only way to learn to judge and record female reproductive states. On this record

sheet, note also the date of any changes in reproductive state, to be included in the monthly demographic summary.

Although it is perhaps easy to view the changes in these codes as part of a predictable cycle, do not be tempted to infer the next code to use based on what you expect is happening. Always assess the swelling and colour of the paracallosal skin objectively. Also note that some females are idiosyncratic, and their characteristics must be learnt with experience.

Barton used a different system for categorising female sexual states (see Appendix I), but now the technique used by Strum and UNBP is employed.

If adult females are not the focus of your specific project, then this basic data collection could be part of the routine of the field assistant, but again there will be days when you will be alone in the field and have to be competent at collecting these data. As with the daily census, work this into the routine of your day.

At present, body condition for members of STT is recorded once a week (?) by members of Shirley's team in conjunction with Charles King'waa (Andy's field assistant) to ensure consistency in the assessment. The method and codes they use follow those developed by Robert Barton in his study (see Appendix I). A copy of these data should be kept in STT files. Some female sexual state sheets have room to record body condition too, but unless the method being employed at the moment changes, there is no need to complete that part of the sheet.

1.3 AD LIBITUM NOTES:

Data collected in this way is the source of most of the information recorded on the life history, predation and intertroop interaction sheets, as well as providing important information about grooming and other affiliative behaviours, copulations, aggression and avoidance, consorts etc., and general troop movements and behaviour.

Individual field workers vary in how they like to collect ad lib notes. Some people like a structured sheet to complete, and others

prefer a blank sheet of paper. UNBP and Andy's field assistant have been taught the same system by Shirley Strum of how to make ad lib notes, so it is a good idea to note what they do during your first weeks in the field and to then adopt a technique that suits you. Appendix III contains a copy of the codes that Andy's field assistant, Charles (Francis) King'waa, uses (derived from those used by Strum). It is recommended that you familiarise yourself with these or devise a standard code that suits you, in order to quickly and consisely record ad lib. data.

There is some important information that must be recorded in these notes: 1) date; 2) time of arrival; 3) sleeping site where the troop was located; 4) time the baboons descended from the trees or rocks (or the fact that they had already descended by the time of arrival); 5) time the troop started to move away; 6) time of arrival at sleeping site in the evening; 7) time of ascent; 8) time of departure from the baboons.

Beyond this, detailed notes should be made on any troop interactions, predations etc. as far as is possible within the schedule of focal data collection, to be distilled onto the appropriate Project record sheets. Ad lib. data on groomings and social interactions are especially important as they provide information on potential relatives and rank. Any unusual interactions should be documented as completely as possible, using codes to enable the whole sequence of events to be recorded concisely (see Appendix III). Similarly, details of any unusual occurrences, for example births or unusual troop behaviour, should be noted as fully as possible.

1.4 INDIVIDUAL LIFE HISTORY RECORDS:

Each individual baboon in our troops has a separate life history sheet (plus extra ones if necessary), recording personal details and life events for that individual. A new sheet is started for every live birth and for any previously unknown individual which transfers into the study troops. Suitable information from ad lib. notes should regularly be recorded on this sheet.

The following are guiding points.

Troop: always STT followed by '1' ('LAMBAA') or '2' ('MBUNI'). If a male migrates to another troop, when you are confident that the change is permanent, alter this part on his record.

Name: Each baboon has one unique name, preferably starting with the first letter of the mother's name and one other from her name, or whatever is most appropriate to denote the close relationship.

ID Code: 2 letters - usually first letter plus one other from the name. Codes should never be duplicated. There is a list at Chololo of all the ID codes which have already been used. If the most suitable code has been used before, then pick another that is appropriate, where ever possible including the code letters in the name.

Birthdate: Exact date if known, but if the birth was not observed, enter the dates when the mother was last seen and when the infant first seen as the range of dates when birth could have occurred.

Known kin: In this section, only 100% certain kin are recorded - i.e. usually only relationships through the mother. This information must be cross-referenced to other individuals' life history sheets when any new infant is born.

Putative kin: These may be completed from grooming observations and cooperative behaviour. Most likely to be the individual's close social group. Enter this information when you feel confident of your decision and enter who has made the assignment.

Sampled by: This is a record of which workers have recorded data from this individual (not ad-lib records), the dates of the period of study, and the type of data recorded i.e. focal, scan.

Rank: This is currently not recorded for STT. New workers may consider completing this section if it will not influence their data collection. (It is generally not a good idea; we can always reconstruct from observations later on. Each new observer should be "naive" if rank effects are of interest. Rank is then computed during data analysis after data collection is complete.)

The following information is entered on the life history sheets on a day-to-day basis and is additionally summarised on the monthly demographic summary sheets (see below).

Injuries: Details of any injuries to that individual with any necessary explanatory comments.

Demographic transitions: Enter here details of significant life events which mark the current stage of life, with the corresponding date: i.e. transfers to and from troops; developmental changes (infant/ juvenile/ sub-adult/ adult, as described and defined in Appendix II); reproductive events, e.g. becoming pregnant, giving birth.

1.5 PREDATION SUMMARY:

These sheets originate from Shirley's interest in predation, and are maintained to keep a long-term record of these events in STT troop. The following are some extra notes on the type of ad lib. data to collect in the event of a predation, and details to be completed on the checksheet at the end of the day.

Location/ cover: Location is the grid reference at which the predation took place. Cover is the type of habitat there. For list of codes for habitat type see Appendix IV.

Capture seen: Yes or No?

Type of capture: Was the capture a chase, a stalk and chase, or a seizure, and who did it?

Consumption: IDs of individuals involved in consumption of the captured prey, including those that just attended the consumption.

Comments: Where was the troop in relation to the kill? Did the prey scream? What was the response of the other prey? Was there any sharing or stealing of food? What order was the consumption of the carcass? Did they eat the brain, and how did they get to it?

1.6 INTER-TROOP ENCOUNTERS:

These records are completed whenever an inter-troop meeting occurs. The following are notes on the type of field ad lib. data to collect, which are then entered on the sheet at the end of the day.

Troop/ Loc.: Which troops and where were they located?

Inct.: Was there any incentive for the encounter? e.g. were they both going to water etc.?

Herding: Did any of the males herd (chase) any females?

Aggression: Any aggression between members of the two troops?

Friendly: Any greetings or play between members of the two troops?

Cop. etc.: Any copulations between members of the two troops?

Vigilance: Who was vigilant of the other troop?

No Int.: No interaction - Yes or No? Even though they could hear and see each other did they not come in contact and respond to the other troop?

Outcome: Which troop avoided or was displaced by the other?

1.7 RANGING DATA:

Ranging behaviour of the troops is assessed using a map of the home range of the troops which is divided into $1/4 \text{ km}^2$ squares. The grid reference of the square which the centre of the troop occupies is recorded regularly throughout the day (e.g. every 15, 30 or 60 minutes). These data can be recorded on check sheets, or using a hand-held computer and the 'MBUNI' computer program. They are then used to calculate the length of day journey and patterns in use of home range areas.

2. Monthly demographic summary

This is a comprehensive summary of troop demography, completed for every month on each troop, usually within the first few days of the next month. It is most important for the long-term records of Chololo. Details are recorded on 2 sheets under the various headings listed below and are derived from the census and sexual state records of those baboons present during and at the end of the month, and from the day-to-day records made as ad lib. notes (also recorded on the life history sheets). When completing these sheets, make a rough copy first and discuss the summary with any co-workers, incorporating their contributions. The following are some guiding points (and see completed example in Appendix V).

Troop size:

In this section enter information on the numbers of baboons in the whole troop and in each age-sex category. For descriptions and definitions of the category classifications see Appendix II. This section is rather complex, so be sure that you understand what figures are required in each section.

Real/demographic n: This is a feature of Shirley's records where there has been intervention to prevent the death of some baboons. 'Real' n is the actual number of baboons alive: 'demographic' n is the number available for study (i.e. minus those which are demographically dead). There is no intervention with STT troops, so this distinction is unnecessary for us - therefore complete only the left hand side of this section, and enter the total number of baboons in the troop as the real n.

Troop count represents those present at the end of the month, but with these additional qualifiers:

- i) If an animal dies, it is counted as IN the troop if it is alive for > 15 days that month : <= 15 days means the animal is counted as out.
- ii) If an individual is with the troop for 15 days or less in the month, it is NOT counted as a member of the troop that month.
- iii) If the observer is not with the group for the majority of the month (less than 16 days) then count individuals as in or out based on whether they were with the troop more or less than 50% of the time - 51%

is counted IN: 50% or less is counted OUT.

iv) If you are with the troop for only a few days in a month, decide on group membership based on last month's list and make a note of who you saw on those few days.

v) Infants are counted IN in the month in which they are born, no matter what the birthdate is.

Troop demographic data is recorded separately for each age-sex category within the troop. A first broad division is made between males, females, juveniles and infants, with the data for these categories recorded on separate lines. These categories are then subdivided. For males and females, the line is divided into two developmental categories, adults and sub-adults, where the number in each category is recorded. For juveniles and infants, the line is divided into males and females, where the number of each is recorded.

For females: Record also the number of adult and subadult females who are cycling, pregnant or lactating in the lines below (by definition, no subadults should be lactating of course). This should equal the total no. in the 'female' line above. The number of females 'cycling' is based on the sexual state of females on the last day of observation of that month. This figure includes females who must have become pregnant during that month (determined retrospectively) but who were not noticeably so on the last day of the month.

For infants: Record also the subtotal of all infants (male and female) who are black infants in parentheses on the next line. Don't think that 'infants' are brown infants in contrast with black infants. 'Infants' is a total (black infants a subtotal already included in the line above).

N.B. The information in the rest of this summary should cross-reference with that recorded in the individual life history sheets so that all the long-term records are accurate and up-to-date.

Births:

Enter details and as much additional information as possible. All births are recorded, even if the infant dies shortly after birth. (In that case the infant may just be referred to as an unnamed 'black

infant'.)

Transfers:

The table is divided into two sections: transfers IN and OUT. Record all the dates for transfers in and out of the troop, whether the transfer is permanent or not. If possible, also record the troop which the individual has migrated to or from.

Deaths:

Enter as many details as possible.

Injuries:

Enter details, with comments as to the circumstances of the occurrence. Also enter notes on any long term injuries/ progress of a previous injury.

Transitions and changes:

Details of individuals' developmental changes or changes in reproductive state that occurred during that month, for example, a black infant becoming a brown infant; a juvenile being promoted to a subadult; a female becoming pregnant, giving birth or resuming cycling. These changes MUST mean differences in the numbers of baboons in the different age-sex categories and female reproductive states from the previous month's record, so check this.

Interventions:

Currently unnecessary to record anything here for STT.

Notes and comments:

Record any unusual occurrences or information helpful in long-term analyses, for example, changes in troop ranging patterns/sleeping sites, or the effects of local people etc..

On the back of the second sheet: list by ID all members of the troop who

have been present at all during the month, in their appropriate age-sex categories. If this list is different from that of the previous month (i.e. any transitions, changes, or transfers), mark the relevant IDs with a + or - sign to denote the change. The total numbers of individuals in each category should be identical to those in the 'troop size' section, with the exception of individuals who are counted as 'OUT' although they have been recorded as present in the troop on the daily census for some days in the month. Again these should be marked so as to explain the discrepancy. Mark the total number here, though this may not be the same as the value in the 'real n' section.

3. Ecological monitoring

3.1 DAILY RAINFALL AND TEMPERATURE MEASUREMENTS:

Daily rainfall and max. and min. temperatures in the shade are recorded by Shirley's staff in a book at Chololo. Make sure you have a copy, and that a copy is brought back for the long-term records kept in St. Andrews.

3.2 MONTHLY ECOLOGICAL MONITORING: (adapted from Barton 1989)

Two days each month are spent monitoring plant phenology and productivity using a number of techniques. These involve measuring the total herb-layer green biomass, the baboon foods found in the herb-layer, and the baboon foods in trees and shrubs.

Robert Barton and Liz Anderson, Andy's assistant, established three permanent transects in 1986, two of 2 km and one of 1 km in length (Transects A - C: Rough Rocks, White Rocks and Mali respectively), and in 1988 a fourth 1km long one was added by Isy Saunders (Transect D: Fever Tree Gulley) (see diagrams and grid references in Appendix IV for exact locations). In April 1990, the ecological monitoring was streamlined, so at present we collect data from Transect A and selected points on Transects B - D. The transects are located in such a way as to provide a representative sample of habitat types within the baboons' home range (see Appendix IV for definitions of habitat types). The transects are

oriented either north-south or east-west, and cairns are built at 200m intervals along them providing a total of 34 permanent points of which 24 are currently being sampled (plus 2 on Transect C for total herb-layer green biomass only).

At each sampling point, the following techniques are used.

3.2.1 Total herb-layer green biomass:

Fluctuations in the gross biomass of green herbiage are assessed using the pin-frame method originally described by McNaughton (1979) and used by Shirley Strum/ UNBP. Collecting data at points on our transects using this technique thus generates data comparable to those from UNBP. Also, using this technique in addition to more detailed estimates of biomass at the same sites means that the different techniques can be compared and used to validate each other.

The pin-frame method is straight forward and simple to perform. The pin-frame itself consists of two wooden 'A' frames which support a horizontal ridge bar, and four long wire pins which are randomly slotted down through a row of holes in the ridge bar. A count is made of the number of contacts between green and brown plant material and the pins, anywhere along the length of the pin.

Data are collected using this technique at two sample points on each transect A - D, a total of 8 sample points. At each sample point, the pin-frame is placed on each of the four main compass bearings, about 1 meter from the cairn in two consecutive positions. After each set of four pins, the position of the pins are changed randomly. In total, 8 pin counts are recorded for each bearing, i.e. 32 counts per sample point.

Data are recorded in separate columns for green and brown plant material. The check sheet used has been designed so that for each sample point, the count for each of the 32 pins occupies a separate line. See Appendix V for an example of a completed data sheet.

Green biomass (B) estimations for the home range of the baboons can then be computed from the mean number of hits per pin using the following equation:

$$B = 6.3 + 16.93(h)$$

where h is mean hits per pin (McNaughton, 1979). (Ideally, because of differences in vegetation structure, the equation should be calibrated with clipped biomass figures from the particular study site but the calibration is the same from Serengeti to Amboseli so it is unlikely to be different here. Anyway, since the main concern is with temporal variation within the site, rather than with the absolute values of the biomass figures, this is not critical.)

3.2.2 Herb-layer baboon food biomass:

The biomass of baboon foods found in the herb-layer or loose on the ground (g/m^2) is assessed each month by using a $1/4 \text{ m}^2$ portable wooden quadrat. The quadrat is placed on the ground at two places at each sample point, giving a total of 48 quadrats in the home range of the baboons, equivalent to a sample area of 12m^2 . Biomass can not be measured directly by removing foods for weighing because data are collected at the same spots each month. Instead, the numbers of items of each type of food are counted within the quadrat, and in order to estimate biomass, these counts are multiplied by the values of dry weight per item which have been obtained for each type of baboon food from sites away from the sample points.

Samples of most known baboon foods have been collected for phytochemical analysis by Rob Barton and Andy Whiten, thus providing dry weight values for average 'bites' or items of many food species. With any new baboon foods, take a sample of at least a hundred 'bites' or items as you have observed the baboons doing in order to calculate the dry weight value of an item (see Plant material collection section below (3.3)).

The following are some guiding notes on collecting these data and completing the check sheets (see also the example in Appendix V):

Positioning of the $1/4\text{m}^2$ quadrat: The quadrat is placed on the

ground adjacent to marker pegs on either side of the cairn. The pegs are located 1m from the cairn at 90° to the direction of the transect. At some sample points, the pegs may have been removed, in which case pace out the distance from the cairn, and replace the missing pegs as soon as is feasible. The bottom left- or right-hand corner of the quadrat is placed on the outside of the peg with the quadrat extending in the direction of the transect. The exact positioning of the quadrat therefore varies between transects: this is illustrated by the diagrams in Appendix VI. For each quadrat, record the sample point and which position relative to the cairn the data are being collected from.

% Green: For each quadrat, assess the 'greenness' of the plant matter that is present in the quadrat on the scale of 0 - 4 (0%, 1-25%, 26-50%, 51-75%, 76-100%). This is NOT a measure of what proportion of the quadrat is covered by living plants, rather it is an assessment of the quality of the plant material that is present. (The amount of plant material is assessed for each species separately by counting the number of plants.)

Herbs / Grasses: In this section, detailed data on each living plant within the quadrat are recorded. Do not count any plants which grow into the quadrat from outside it.

As far as possible, identify every living plant. Record its name or the code which has been assigned to it while waiting for samples to be identified by the herbarium. If there are any new unidentified plants in the quadrat, assign a code to the plant, write a description of the distinguishing characteristics of the plant and its habitat, note the sample point where it was found, and take at least two good samples of the plant from outside the quadrat so that samples can be prepared to send to the herbarium (see also the Herbarium's notes on collecting and preparing samples). The best samples are those which include a flower, so it is probably worth waiting till after the rains to collect a good sample of any new plants, but meantime be sure that you have a recognisable sample or description so that you can locate the plant again. If the living plant is unrecognisable, record its presence with the codes for unidentifiable herb/grass etc. When you cannot identify a plant, do not infer what you think it is: use the codes for unidentifiable.

For each species of plant, record the number of plants present. If it is a grass species where there are too many plants to count accurately e.g. *Penisetum* species, then record the amount of plants as a percentage of the quadrat covered by the plant e.g. 50%.

For each plant species, assess the amount of leaves, flowers, fruits/seeds and flower buds on a scale of 0 - 4 (0%, 1-25%, 26-50%, 51-75%, 76-100%). For the assessment of leaves the scale is 1 - 4 as 0 would mean that the plant was not living. This rating is a measure of these parts of the plant as a proportion of their potential maximum amount, for example the amount of leaves as a proportion of the maximum leaf growth that plants that size might exhibit, or the amount of fruits present as a proportion of the maximum number of fruits such a plant might produce. It is often difficult to assess this until you have some experience of the fluctuations in growth and production that these plants exhibit (see also the section on the estimation of baboon food in trees and shrubs): be guided by the current fieldworkers until you learn to make these distinctions reliably accurately. At Chololo there is also a book of photographs showing examples although these are mostly shrubs and trees. N.B. The nature of the assessment here is different from the rating used in the assessment of % Green. The % Green rating assesses the quality (the 'greenness') of the plants, so it is possible to have a % Green rating of 1 and a rating for leaves of 4 where the leaves are very brown, but the amount of them is close to the maximum amount that a plant that size could produce.

For these columns on the checksheet, if the rating is non-zero, then divide the square diagonally into two, and write the rating in the lower half.

For all baboon food plant species present, a count or estimation of the number of 'bites' or units of the edible parts (e.g. fruit or seeds, grass blades, bases, grass flowers etc.) is recorded. In many cases, where items of food comprise discrete units (such as with individual flowers, fruits and leaves) this procedure is straightforward. In the case of grass blades, however, estimates are a little cruder, because it is not feasible to count each individual blade: the number of average-sized (adult female) baboon bites of grass blades available in the quadrat are counted, where the estimation of bite-size is based on observations of the animals feeding. The number of baboon 'bites' of

food present in the quadrat is written in the upper half of the divided square in these columns. If the plant species is NOT a baboon food, then enter a diagonal slash to show that there are no missing data. If the part of the plant that is eaten is something other than these parts e.g. the succulent bases of some *Commelina* species, and the bases of the grass *Mariscus*, then enter the number of items present in the quadrat for this species under the column of 'other' and clearly note the part that is eaten. Non-growing items that the baboons picked up from the ground, such as dried *Acacia* flowers and seeds, are also noted, at the base of the checksheet. These data are multiplied by the appropriate dry weight values in order to calculate the biomass of herb-layer baboon food.

N.B. When rating the amount of fruits, flowers, or flower buds, assess all that are present, including any dead or dry ones. However, when counting the number of 'bites' of baboon food, include only those which are edible, i.e. fresh pods/fruits, flowers, and grass blades.

For food species where estimated 'bites' of the food are used to measure the biomass of baboon food present e.g. grass blades, it is a good idea to check your values by comparing the predicted biomass value calculated by estimating the number of bites in a test quadrat and multiplying this by the dry weight values, with the actual biomass of the quadrat measured by harvesting all edible blades there. During this test, you can also check that the dry weight of your estimated adult female-sized 'bite' is similar to that used by Barton, by collecting a known number of 'bites' of the food and then drying and weighing them to calculate the dry weight value of one 'bite'.

3.2.3 Baboon food biomass in trees and shrubs:

The biomass of baboon foods available from trees and shrubs is assessed by estimating the dry weight of food present in focal trees and shrubs, and multiplying these values by the density of such species within the home range.

At each sample point, 4 focal trees and 4 focal shrubs are examined every month. Four quadrants are delineated by the bearings of the four main compass points from the cairn, and within each of these quadrants,

the nearest tree and the nearest shrub over 50cm high have been selected and marked (originally by Barton and Anderson) as the focal trees and shrubs. The amount of baboon food present on each of these is counted or estimated and recorded on the checksheets. These values are then multiplied by the values of dry weight per item which have been obtained from other trees in the home range, in order to calculate the average dry weight of food items per tree or shrub of a given species.

The following are guiding points for collecting these data and for completing the checksheet (see also the completed sheet in 's Appendix V).

Locating the focal trees and shrubs: The compass quadrants at each sample point are numbered (1 - 4). No. 1 quadrant is always the first clockwise quadrant when facing in the direction of the transect. Since the direction of the transect varies on the different transects, the numbering of the quadrants is not fixed in relation to North. Diagrams in Appendix IV illustrate the numbering of these quadrants for each transect. Within each quadrant, the focal trees and shrubs are marked with red tape (old) and pale green paint. The species of the focal tree or shrub and their bearing and distance from the cairn is marked on the checksheet to accurately identify them.

If a focal tree or shrub cannot be located, it is possible that it has died or been destroyed. If this is definitely the case, it should be replaced by the nearest tree or shrub in the same quadrant. Measure the distance from the cairn to the new focal tree/shrub, and take its bearing. Make a note of the change and these new details on the checksheet, and amend future sheets. Mark the new tree/shrub with paint as soon as possible. Do not be misled into thinking that dry or dormant trees/shrubs are dead: wait several months before pronouncing it dead. Once a replacement focal has been allocated, do not return to the previous one, even if it becomes rejuvenated.

For each focal tree and shrub: assess the amount of leaves, flowers, fruits/pods and flower buds on a scale of 0 - 4 (0%, 1-25%, 26-50%, 51-75%, 76-100%). This is similar to the assessment of plants in the herb-layer, where the rating is a measure of these parts of the tree/shrub (including dead/dry parts) as a proportion of their potential maximum amount. For trees and shrubs however, the assessment of leaves

is a measure of percentage of leaf coverage and the quality of the leaves (in contrast with the nature of this assessment of plants in the herb-layer). These assessments are difficult to make until you have some experience of the fluctuations in growth and production that are exhibited. At Chololo there is a file of photographs with examples of trees and shrubs of different species which demonstrate the various ratings. Use this as a guide for making these assessments, and test your assessments with the current fieldworkers. Each tree or shrub must be treated individually: although the ratings are fairly clearly defined, different trees and shrubs will exhibit different types of change. N. B. The shrub *Sansevieria intermedia* is very hard to assess, and the application of the ratings 0 - 4 must be learnt with patience. Rating leaves for this shrub is an assessment of the quality of the plant, its greenness/juiciness/edibility.

As with measures of biomass in the herb-layer, if these ratings are non-zero, the square on the checksheet is divided diagonally into two and the rating written in the lower half.

If these parts of the trees and shrubs are known or suspected baboon foods, count the total numbers of edible items (flowers, pods etc.). This is similar to the counts of baboon food in the herb-layer, and involves counting only parts that are in an edible state. When numbers are too great to count directly, estimate the number of items present in the following ways. For shrubs and smaller trees, the number of items on several branches can be counted, the average number per branch calculated, and this figure multiplied by the total number of branches. For trees too large to make counting of every branch feasible, the number of branches in a vertical section, two arm-spans in width, can be counted and multiplied by the number of those sections in the tree. Practise your estimations with other fieldworkers, checking them with actual counts when possible, so that your assessments are accurate and objective.

The number of items of baboon food is written in the upper half of the appropriate square on the checksheet. If the part of the focal tree or shrub is not a baboon food, then a diagonal slash is entered to show there is no missing data.

Tree and shrub density in the home range is estimated every few years by recording the occurrence of each tree and shrub species in quadrats of 30 x 30 m at each of the sample points. The tree and shrub densities for the home range (average number of individuals of each species per m²), can then be used in conjunction with the values of average dry weight of baboon food per tree or shrub of a given species to calculate the biomass of baboon food in trees and shrubs. The 30 x 30 m quadrats are situated in the No. 1 compass quadrant at the cairn (see diagrams in Appendix IV for location of compass quadrants on each transect). In 1990, Whiten decided that counting the number of shrubs in a 900m² area was impractical, so shrub density was estimated in a smaller area consisting of four 10 x 10 m quadrats, one at each corner of the 30 x 30 m quadrat, while counts of the tree species present were made in the larger area. (Barton made counts for different sizes of tree and shrub for a more detailed calculation of biomass in trees and shrubs.)

For some species of tree which do not appear in any of the quadrats because their distribution is very clumped e.g. *Euphorbia nyikae*, count the total number of these trees within the home range, and calculate their density by dividing by the home range size. For such species, biomass (B) is then given by

$$B=w(n)/HRS$$

where w is the mean dry weight of pads (grams), n is the estimated number of segments within the home range, and HRS is the home range size (m²). (In using the same biomass estimate for each month we assume that availability does not vary during the study period.)

3.2.4 Baboon food biomass from underground items:

Assessment of underground food items is highly problematic: the obvious way is to dig up quadrats and extract, dry and weigh all food items found, but because we return to the same sample points each month this is not feasible.

Instead, the density of such plants is measured using the 1/4 m² for plants with edible corms and bases like *Cyperus blysmoides* and *Mariscus amauiropus*, and by the method described above for the shrub *Sansevieria intermedia*. The mean number of edible corms per plant for *Cyperus blysmoides* is estimated by counting the number of plants in a

small quadrat (0.1 m^2) away from the transects, digging this up to a depth of six inches, passing the soil through a fine wire mesh, and counting the number of corms thus extracted. Not all bases of *Mariscus amauiropus* and *Sansevieria intermedia* are edible (baboons seem to be very selective in the ones they pull up) so counts made in the $1/4 \text{ m}^2$ quadrats have to be corrected by assessing the proportion of bases that are edible in a random sample away from the sample points. The number of edible bases and corms can then be multiplied by their dry weight values and by their density in the home range in order to estimate the baboon food biomass from such underground items.

3.2.5 Large mammal counts:

The livestock and wildlife within the home range of the baboons is also monitored every month. All sightings of animals from specified points and while walking the transects are recorded for Chololo and for the Reserve.

Transects A and C (Chololo):

- 1) The drive from the Chololo sign board near Geoffry's House to Rough Rocks, and the drive from Rough Rocks to the head of Transect C.
- 2) Two points on top of Rough Rocks (looking East and West, where the maximum area can be seen).
- 3) Along the length of the transects.

Transects B and D (the Reserve):

- 1) The drive along the main road from the school turning (850415) to White Rocks, and the drive from White Rocks to Fever Tree Gulley.
- 2) Two points at White Rocks (looking North and South-East, where the maximum area can be seen).
- 3) Along the length of the transects.

Sightings of animals made at each of these points is independent from sightings made at the others, so groups of animals can be recorded more than once from different view points. Use binoculars to see as much as possible.

These data are summarised on the large mammal count checksheets (see Appendix V). Record also any sightings of predators or elephants made during the month, and any additional information, e.g. cattle movements.

3.3 PLANT MATERIAL COLLECTION AND PHYTOCHEMISTRY

Samples of new plant material should be collected whenever possible. In the case of baboon foods, the number of items or bites should be counted as the plants are harvested. The samples are immediately sealed in plastic bags and weighed. Samples are subsequently dried to constant weight in the sun in a secure sheltered place or in a drying chamber. For each sample a record is kept of the collection date, the fresh weight, the dry weight and the number of items or bites. The samples are then tied up in fresh plastic bags and stored in a canvas sack inside a dry, dark cupboard. They should be checked periodically for signs of dampness or degradation.

**APPENDIX I: DIAGRAMS AND DEFINITIONS OF FEMALE REPRODUCTIVE STATES; CODES
FOR BODY CONDITION.**

- (i) Female reproductive states: new codes (SCS 8/90)
- (ii) Female sexual state categories used by Barton (1989)
- (iii) Female body condition codes (Barton, 1989)

(i) Female reproductive states: new codes (SCS 8/90):

FEMALE REPRODUCTIVE STATES: NEW CODES 8/90 *modified from 15/JS 1977 for a.d. 70*

I. NON-SWOLLEN

- 0 - FLAT, CYCLING
- 7 - MENSTRUATING
- 8 - PROGNANT
- 9 - NON-CYCLING & NOT PREGNANT

COLOR ASSESSMENT

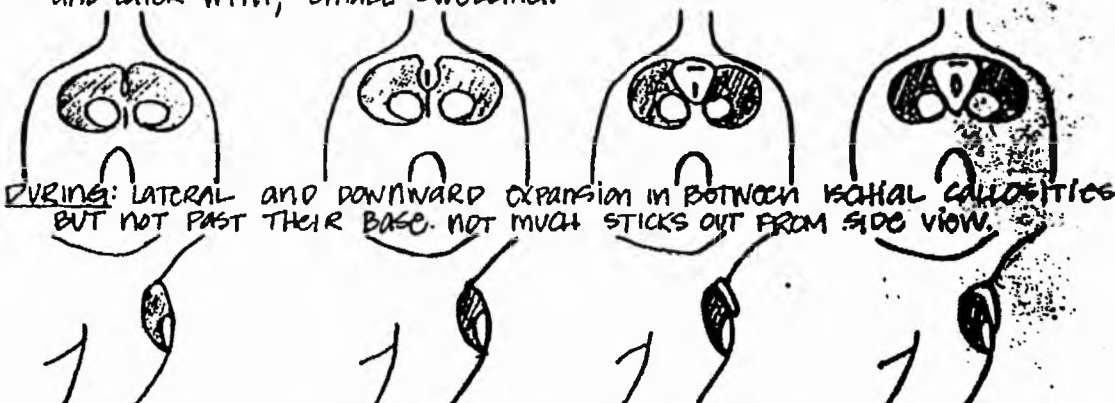
- 0 - NO ASSESSMENT MADE
- 1 - ALL GREY
- 2 - MOSTLY GREY, LITTLE PINK
- 3 - 1/2 GREY, 1/2 PINK
- 4 - MOSTLY PINK, LITTLE GREY

- 5 - ALL PINK, PALE
- 6 - ALL PINK, MEDIUM
- 7 - ALL PINK, INTENSE
- 8 - PINKISH GREY

II. SWOLLEN

10 → 20 → 30 → 40 → 50 SIZE OF SWELLING INCREASES, CAUSING EXPANSION DOWNWARDS, SIDeways, AND BACKWARDS. WHEN IT PUSHES UP THE TAIL, IT GETS MORE WRINKLED IN THAT AREA. WHEN IT GETS BIGGER DOWNWARDS, THERE ARE NO WRINKLES.

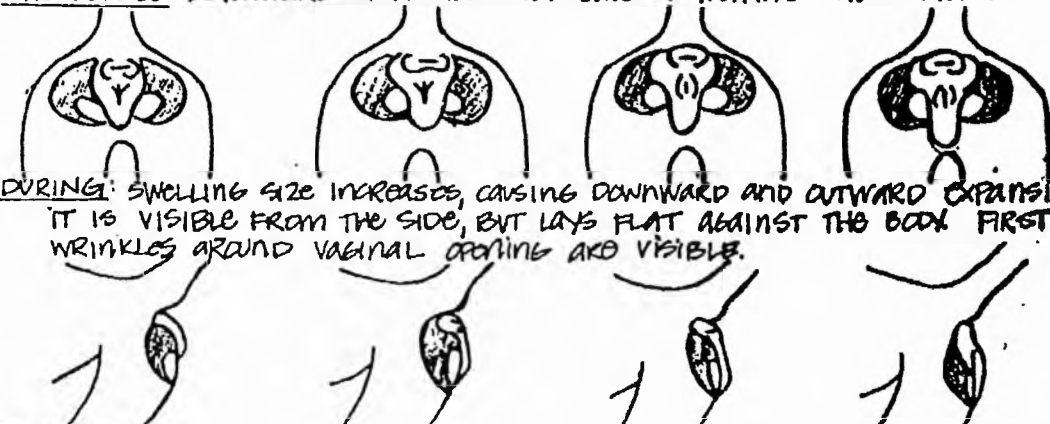
SWOLLEN 10: SMALLEST SIZE SWELLING CATEGORY. VAGINAL ENLARGEMENT WITHOUT AND LATER WITH, SMALL SWELLING.



DURING: LATERAL AND DOWNWARD EXPANSION IN BETWEEN ISCHIAL CALLOSITIES BUT NOT PAST THEIR BASE. NOT MUCH STICKS OUT FROM SIDE VIEW.

10 → 20: SIZE AND EXPANSION LATERAL AND DOWNWARDS.

SWOLLEN 20: DOWNWARD EXPANSION PAST BASE OF ISCHIAL CALLOSITIES.



DURING: SWELLING SIZE INCREASES, CAUSING DOWNWARD AND OUTWARD EXPANSION. IT IS VISIBLE FROM THE SIDE, BUT LAYS FLAT AGAINST THE BODY. FIRST WRINKLES AROUND VAGINAL OPENING ARE VISIBLE.

20 → 30: SIZE AND EXPANSION BACKWARD, ESPECIALLY LARGER FROM THE SIDE.

SWOLLEN 30: UPWARD AND BACKWARD EXPANSION AWAY FROM THE BODY ESPECIALLY VISIBLE FROM THE SIDE BY COMPARISON WITH #20's.



DURING: SWOLLING SIZE INCREASES WITH EXPANSION IN ALL DIRECTIONS: UPWARDS UNDER BASE OF THE TAIL CAUSING MORE WRINKLES, AND DOWNWARD BETWEEN THE LEGS.



30-40: SIZE AND EXPANSION Laterally and BACKWARD.

SWOLLEN 40: SIDeways and UPWARD expansion. SWOLLING IS MUCH LARGER THAN #30's WHEN VIEWED FROM THE SIDE.



DURING: ENLARGED VOLUME. FROM THE SIDE, SWOLLING BECOMES VISIBLE PAST THE TAIL



40-50: SIZE AND ESPECIALLY BACKWARD EXPANSION.

SWOLLEN 50: LARGEST SIZE WE HAVE EVER SEEN - MUCH LARGER THAN #40's. USUALLY ONLY ADOLESCENT FEMALES.



MENSTRUATING:

- 70 - NO SWELLING.
- 72 - EQUIVALENT TO ANY SWELLING.
- 79 - UNSPECIFIED CATEGORY #20

DEFLATING: RETURNS CORN OF ANY DEGREE.

- 62 - VERY SLIGHT DEFLATION, NOTICEABLE WRINKLES (SLIGHT).
- 64 - NOTICEABLE DEFLATION, EQUIVALENT TO A SWOLLEN 30 BUT WRINKLED
- 66 - NOTICEABLE DEFLATION, EQUIVALENT TO A SWOLLEN 10 OR 20.
- 68 - NEARLY FLAT, VERY SLIGHT SWELLING STILL VISIBLE.

(ii) Female sexual state categories used by Robert Barton (from Barton (1989), Figure 2.5):

A. SWOLLEN

Numbers 1-5 represent increasing degrees of swollenness of the sexual skin as the cycle progresses. Ovulation occurs in the later stages of swelling, but there is substantial individual and seasonal variation in the maximum size reached.

- 1: Vaginal enlargement with or without slight swelling.
- 2: Downward expansion of swelling to bottom of ischial callosities.
- 3: Backward expansion, visible from side.
- 4: Lateral expansion, with or without further descent.
- 5: More expanded version of 4.
- 6: Detumescent.

B. MENSTRUATING: menstrual blood visible prior to swelling.

C. PREGNANT

D. LACTATIONAL AMENORRHEA

- 1: Infant with natal coat colour (black).
- 2: Infant with transitional coat colour.
- 3: Infant brown.

(iii) Female body condition categories used by Robert Barton (from Barton (1989), Figure 2.6):

A. NO OBSERVABLE WEIGHT LOSS

- * 1: No hair loss
- 2: Some hair loss
- 3: Extensive hair loss

B. NOTICEABLY THIN

Narrowed waist, relatively high bone definition.

- 1 - 3: Same hair loss categories.

C. VERY THIN

Excessively narrowed waist, pelvic and other bones protrusive.

- 1 - 3: Same hair loss categories.

* Hair loss and weight loss were correlated, so that, for example, a score of C1 (very thin, no hair loss) is unlikely.

At Chololo there is a book of photographs of several of these states, some taken in drought conditions.

APPENDIX II: DEFINITIONS OF AGE-SEX CATEGORIES.

(from Uaso Ngiro Baboon Project/SCS protocol 12/1986)

1) **Infants** are classified as **juveniles** at 2 years of age. This is determined by adding 2 years to their birthdate and changing their status in that month's demographic summary (for example birth in 2/75 is changed to juvenile in summary for 2/77).

2) **Black infants** are classified as **brown** once they are half brown/half black (middle transitional and onwards). Early transitional is still classified as black.

When no coat colour determination is made, infants are classified as brown in the eighth month i.e. add 7 to birth month (born 2/75, brown 9/75).

3) **Females** are classified as **subadult** when they begin cycling (in that month), and remain subadults until the month of the birth of their first infant. At that time they are classified as adults. (***) If a subadult female has a late abortion or miscarriage she is promoted to adult when miscarriage occurs. If she has a miscarriage within the first 2 months, then she remains a subadult until she gives birth next.)

4) **Males** are classified as **subadults** when they visibly show signs of the adolescent growth spurt, i.e. become larger than adult females, usually between 4.5 and 5 years of age. It is best to use their own mothers as markers of adult female size, if the mother is still alive. If not then use a fully adult female relative. If there are none, then use an average sized adult female. The adolescent growth spurt is also indicated by leg length (disproportionally long compared to the body); cape length and acquisition of mantle round face (signs of longer hair below the body and round the face); face shape (becoming adult-like). Males remain subadult until growth ceases entirely and their mane and body hair is completely filled out (around 9 - 10 years of age), when they are then classified as adult.

APPENDIX III: CODES FOR AD LIBITUM DATA COLLECTION:

(derived from those used by SCS)

→	approach
↔	mutual approach
┐	avoid
┘	mutual avoid
+	follow
⊂	walk around
↓	sit
↑	tail up
∞	take ventral
la	look at
lw	look away
pr	present
ht (?)	touch
hg	hip grassp
gr	groom
g	greet
∅	no response
⊖	troop
thr	threaten
ya	yawn
mg	molar grind
✓	chase
✗	chase - no catch
pg	pant grunt
ati	attention to infant
gk	geck
scr	scream
wh	wahoo
ff	fear greeting
mt	mount
1/2 mt	half mount
ps	push to stand
bb	back bite
em	embrace

APPENDIX IV: DEFINITIONS OF HABITAT TYPES; DIAGRAMS OF TRANSECTS.

- (i) Habitat classification system (from Barton 1989)
- (ii) Location and details of transects: positioning of the $1/4\text{m}^2$ quadrats and numbering of the compass quadrants.

(1) Habitat classification system (from Barton (1989), Figure 2.4).

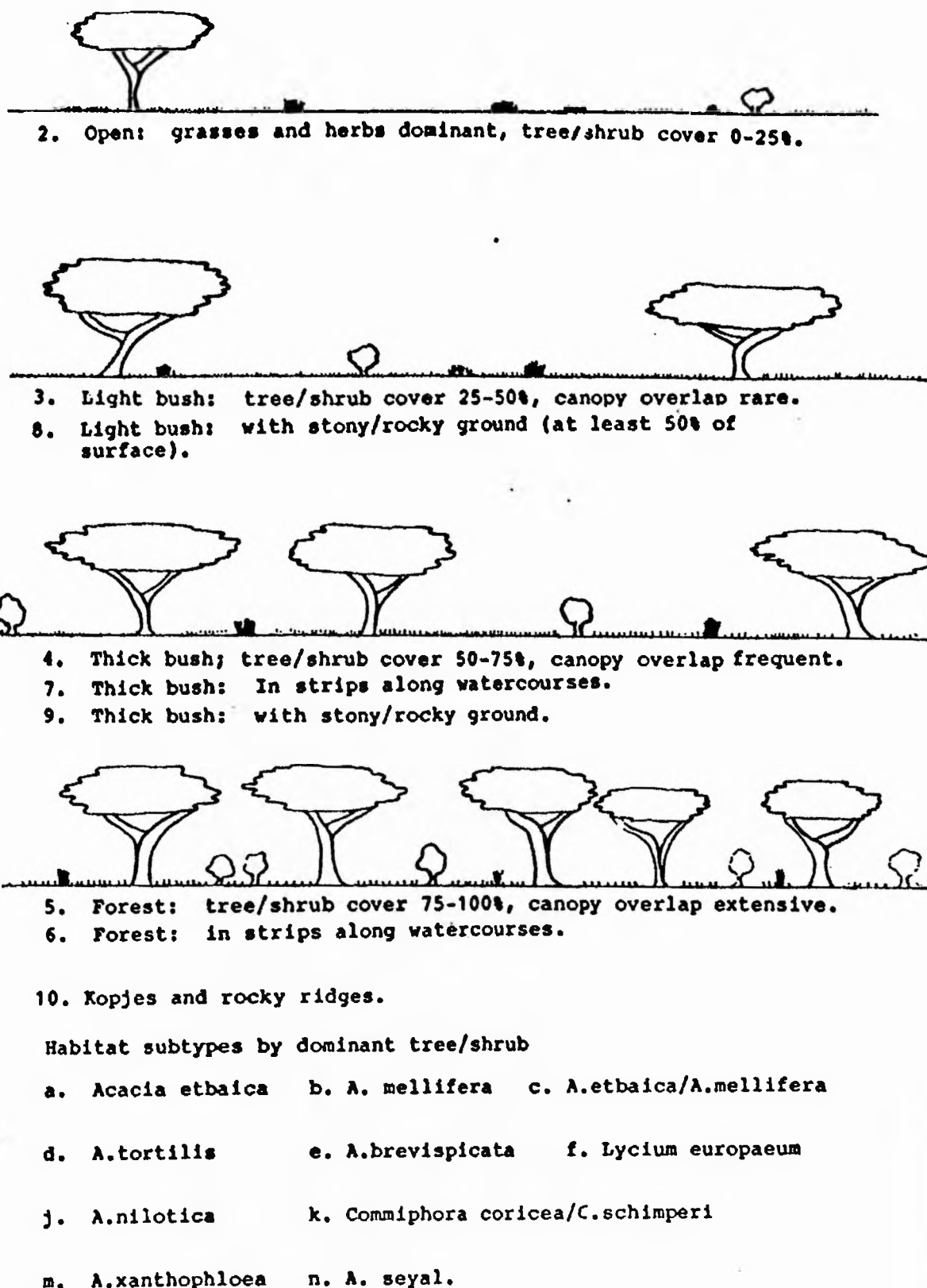


Figure 2.4: Habitat Classification System. Each density type is split into sub-types according to the dominant tree or shrub. Missing sub-types from the table (g,h,i,l) are those that occurred only in very small patches, beneath the resolution of the habitat map.

(ii) Location and details of transects: positioning of the $1/4\text{m}^2$ quadrats and numbering of the compass quadrants.

TRANSECT A: W-E 2 km 820420



TRANSECT B:

N-S 2 km

840440

X10



DIRECTION
OF THE
TRANSECT

TRANSECT C:

N-S 1 km

810440

X10

X10

TRANSECT D: W-E 1 km 860450



APPENDIX V: SAMPLE RECORD SHEETS.

- (i) Daily census
- (ii) Female reproductive cycle states
- (iii) Individual life history record
- (iv) Predation summary
- (v) Inter-troop encounter sheet
- (vi) Monthly demographic summary
- (vii) Herb-layer green biomass (grassland plots) sheet
- (viii) Herb-layer baboon food biomass sheets
- (ix) Tree and shrub baboon food biomass sheets
- (x) Large mammal count sheet

(i) Daily census

1974		1975		1976		1977		1978		1979		1980		1981		1982		1983		1984		1985		1986		1987		1988		1989		1990		1991		1992		1993		1994		1995		1996		1997		1998		1999		2000		2001		2002		2003		2004		2005		2006		2007		2008		2009		2010		2011		2012		2013		2014		2015		2016		2017		2018		2019		2020		2021		2022		2023		2024		2025		2026		2027		2028		2029		2030		2031		2032		2033		2034		2035		2036		2037		2038		2039		2040		2041		2042		2043		2044		2045		2046		2047		2048		2049		2050		2051		2052		2053		2054		2055		2056		2057		2058		2059		2060		2061		2062		2063		2064		2065		2066		2067		2068		2069		2070		2071		2072		2073		2074		2075		2076		2077		2078		2079		2080		2081		2082		2083		2084		2085		2086		2087		2088		2089		2090		2091		2092		2093		2094		2095		2096		2097		2098		2099		2100		2101		2102		2103		2104		2105		2106		2107		2108		2109		2110		2111		2112		2113		2114		2115		2116		2117		2118		2119		2120		2121		2122		2123		2124		2125		2126		2127		2128		2129		2130		2131		2132		2133		2134		2135		2136		2137		2138		2139		2140		2141		2142		2143		2144		2145		2146		2147		2148		2149		2150		2151		2152		2153		2154		2155		2156		2157		2158		2159		2160		2161		2162		2163		2164		2165		2166		2167		2168		2169		2170		2171		2172		2173		2174		2175		2176		2177		2178		2179		2180		2181		2182		2183		2184		2185		2186		2187		2188		2189		2190		2191		2192		2193		2194		2195		2196		2197		2198		2199		2200		2201		2202		2203		2204		2205		2206		2207		2208		2209		2210		2211		2212		2213		2214		2215		2216		2217		2218		2219		2220		2221		2222		2223		2224		2225		2226		2227		2228		2229		2230		2231		2232		2233		2234		2235		2236		2237		2238		2239		2240		2241		2242		2243		2244		2245		2246		2247		2248		2249		2250		2251		2252		2253		2254		2255		2256		2257		2258		2259		2260		2261		2262		2263		2264		2265		2266		2267		2268		2269		2270		2271		2272		2273		2274		2275		2276		2277		2278		2279		2280		2281		2282		2283		2284		2285		2286		2287		2288		2289		2290		2291		2292		2293		2294		2295		2296		2297		2298		2299		2300		2301		2302		2303		2304		2305		2306		2307		2308		2309		2310		2311		2312		2313		2314		2315		2316		2317		2318		2319		2320		2321		2322		2323		2324		2325		2326		2327		2328		2329		2330		2331		2332		2333		2334		2335		2336		2337		2338		2339		2340		2341		2342		2343		2344		2345		2346		2347		2348		2349		2350		2351		2352		2353		2354		2355		2356		2357		2358		2359		2360		2361		2362		2363		2364		2365		2366		2367		2368		2369		2370		2371		2372		2373		2374		2375		2376		2377		2378		2379		2380		2381		2382		2383		2384		2385		2386		2387		2388		2389		2390		2391		2392		2393		2394		2395		2396		2397		2398		2399		2400		2401		2402		2403		2404		2405		2406		2407		2408		2409		2410		2411		2412		2413		2414		2415		2416		2417		2418		2419		2420		2421		2422		2423		2424		2425		2426		2427		2428		2429		2430		2431		2432		2433		2434		2435		2436		2437		2438		2439		2440		2441		2442		2443		2444		2445		2446		2447		2448		2449		2450		2451		2452		2453		2454		2455		2456		2457		2458		2459		2460		2461		2462		2463		2464		2465		2466		2467		2468		2469		2470		2471		2472		2473		2474		2475		2476		2477		2478		2479		2480		2481		2482		2483		2484		2485		2486		2487		2488		2489		2490		2491		2492		2493		2494		2495		2496		2497		2498		2499		2500		2501		2502		2503		2504		2505		2506		2507		2508		2509		2510		2511		2512		2513		2514		2515		2516		2517		2518		2519		2520		2521		2522		2523		2524		2525		2526		2527		2528		2529		2530		2531		2532		2533		2534		2535		2536		2537		2538		2539		2540		2541		2542		2543		2544		2545		2546		2547		2548		2549		2550		2551		2552		2553		2554		2555		2556		2557		2558		2559		2560		2561		2562		2563		2564		2565		2566		2567		2568		2569		2570		2571		2572		2573		2574		2575		2576		2577		2578		2579		2580		2581		2582		2583		2584		2585		2586		2587		2588		2589		2590		2591		2592		2593		2594		2595		2596		2597		2598		2599		2600		2601		2602		2603		2604		2605		2606		2607		2608		2609		2610		2611		2612		2613		2614		2615		2616		2617		2618		2619		2620		2621		2622		2623		2624		2625		2626		2627		2628		2629		2630		2631		2632		2633		2634		2635		2636		2637		2638		2639		2640		2641		2642		2643		2644		2645		2646		2647		2648		2649		2650		2651		2652		2653		2654		2655		2656		2657		2658		2659		2660		2661		2662		2663		2664		2665		2666		2667		2668		2669		2670		2671		2672		2673		2674		2675		2676		2677		2678		2679		2680		2681		2682		2683		2684		2685		2686		2687		2688		2689		2690		2691		2692		2693		2694		2695		2696		2697		2698		2699		2700		2701		2702		2703		2704		2705		2706		2707		2708		2709		2710		2711		2712		2713		2714		2715		2716		2717		2718		2719		2720		2721		2722		2723		2724		2725		2726		2727		2728		2729		2730		2731		2732		2733		2734		2735		2736		2737		2738		2739		2740		2741		2742		2743		2744		2745		2746		2747		2748		2749		2750		2751		2752		2753		2754		2755		2756		2757		2758		2759		2760		2761		2762		2763		2764		2765		2766		2767		2768		2769		2770		2771		2772		2773		2774		2775		2776		2777		2778		2779		2780		2781		2782		2783		2784		2785		2786		2787		2788		2789		2790		2791		2792		2793		2794		2795		2796		2797		2798		2799		2800		2801		2802		2803		2804		2805		2806		28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(11) Female reproductive cycle states

OBSERVATIONS
REMARKS BYFROM
JANK

REPRODUCTIVE CYCLE STATES

TROOP 57T1

MONTH SEPT
YEAR: 1970

ID's	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
9AL				92	92	X	92			92			92	X			92	92		92	92			92	92						
CT				92	92	X	92			92	92	92	X	92			92	92		92	92			92	92						
AN				92	92	X	92			92	92	92	X	92			92	92		92	92			92	92						
EU				87	87	X	87			87	87	87	X	87			87	87		87	87			87	87						
PT				92	92	X	92			92	92	92	X	92			92	92		92	92			92	92						
KE				92	92	X	92			92	92	92	X	92			92	92		92	92			92	92						
KH				72	72	X	72			16	18	24	X	24			28	28		28	28			34	34						
KR				92	92	X	92			92	92	92	X	92			92	92		92	92			92	92						
LZ				91	91	X	91			91	91	91	X	91			91	91		91	91			91	91						
MA				92	92	X	92			92	92	92	X	92			92	92		92	92			92	92						
MA				03	03	X	03			16		24	X				36	36		38	38			61	66						
ME				92	92	X	92			92	92	92	X	92			92	92		92	92			92	92						
MR				18	18	X	18			24		22	X				26	26		26	26			28	28						
NI				03	03	X	03			03		08	X				03	03		84	84			84	84						
OP				87	87	X	87			87		87	X				87	87		87	87			87	87						
SC				92	92	X	92			92	92	91	X	92			92	92		92	92			92	92						
TR				92	92	X	92			92		92	X				92	92		92	92			92	92						
TU				93	93	X	93			93	93	93	X	93			93	93		93	93			93	93						
TW				92	92	X	92			91	91	91	X	91			91	91		91	91			91	91						
WT				03	03	X	03			2	2	2	X				14	14		16	24			24	26						
9ATM				34	34	X	36			36	36		38	X			46	46		64	64			64	64						
CN				28	28	X	32			32	32		34	X			46	46		64	64			64	64						
I				72	01	X	01	01	12	14	16	16	X	64			01	01		01	01			01	01						
ES				26	28	X	32	32	34	34	34	34	X				01	01		01	01			20	32						
GT				86	86	X	87	87	87	87	87	87	X				87	87		87	87			87	87						
JN				74	74	X	62	68	68	68	68	68	X	02			02	02		70	70			14	22						
KY				71	02	X	70	72	72	72	72	72	X				16	18		22	24			26	28						
VS				39	39	X	39	66	66	66	66	66	X				01	01		01	01			01	01						
6/7/70 MK Rec. of Cycle 10/9/70 VS night is pregnant. 20/9/70 VS night is pregnant. ✓ 24/9/70 SP SP gone b.i.t.																															

(iii) Individual life history record

Troop: STT 1

Page 1

LIFE HISTORY

Name: GARLIC (♀)

ID Code: GL

Birthdate: 22/1/86

Mother: GATEAU (GA)

Sampled by:

Dates	Observer	Type of Data
11/87 → 11/90	FOM	FOM

Known Kin (including offspring):

ID	Sex	Date	Relationship
GA	♀	22/1/86	MOTHER
GB	♂	22/1/86	BROTHER
GC	♀	10/10/87	SISTER
GD	♀	30/7/91	SISTER

Rank:

Date Assigned by

Putative Kin:

ID	Sex	Assigned by	Date
GA	♀	FOM	11/90

Injuries:

Date	Type	SS	Comments
------	------	----	----------

13/2/89	cut on right arm		probably from a Madras sparrow when chased from a house.
---------	------------------	--	--

Demographic Transitions:
(Reproduction, Maturation, Migration)

Black infant → Brown infant 31/10/86

Infant → juvenile 22/1/88

Juvenile → sub adult 18/7/90
(first swelling)

Pregnant 31/5/92

Gave birth 27/11/92
(sa. → a♀)

(iv) Predation summary

PREPARED BY

PREDATION: SUMMARY

GILGIL BABOON PROJECT

PG

[illegible]

PREPARED BY _____

INTERTROOP ENCOUNTERS

PG _____

TROOP MONTH YEAR

[illegible]

(v) Inter-troop encounter sheet

(vi) Monthly demographic summary

DEMOGRAPHIC SUMMARY

Date Prepared 4/11/90
Prepared By FIM LNK

TROOP 511 MONTH OCT YEAR 1990

OBS: _____

TROOP SIZE	real n= <u>79</u>		demographic n=	
	adult	subadult	adult	subadult
Males	<u>8</u>	<u>6</u>		
Females				
cycling	<u>7</u>	<u>8</u>		
preg	<u>2</u>	<u>1</u>		
lac	<u>11</u>	<u>—</u>		
Juveniles	<u>11</u>	<u>2</u>		
Infants	<u>8</u>	<u>19</u>		
(Black)	<u>2</u>	<u>4</u>		

BIRTHS

DATE	MOTHER'S NAME (CODE)	INFANT NAME (CODE)	SEX	COMMENT
<u>4/10/90</u>	<u>OPUNTIA</u>	<u>infant confirmed</u>	<u>2 son ♀</u>	<u>and named OTHELLO (OO)</u>
<u>12/10/90</u>	<u>EUPHRODIA (EU)</u>	<u>EUREKA (EA)</u>	<u>♀</u>	

TRANSFERS DATE	ID	IN	AGE/SEX CLASS	OUT	DATE	ID	AGE/SEX CLASS
<u>15/10/90</u>	<u>SA</u>		<u>juv ♂</u>		<u>16/10/90</u>		
<u>27/10/90</u>	<u>90</u>		<u>juv ♂</u>		<u>?</u>		

DEATHS ETC.

DATE	ID	AGE-SEX CLASS	PROBABLE CAUSE
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INTERVENTIONS

DATE	ID	AGE-SEX CLASS	TYPE OF INTERVENTION

(vii) Herb-layer green biomass (grassland plots) sheet

AUG
FNK FEB 1990

GRASSLAND

PLOTS

DATE: 28/6/90
RECORDER: FOM
OBSERVER: TNL

LOCATION: C2			LOCATION: C1		
AREA	GREEN	BROWN	AREA	GREEN	BROWN
NORTH	1 0	III	NORTH	1 0	II
	2 0	IIII		2 0	III
	3 0	III		3 0	0
	4 II	0		4 I	II
	1 0	II		1 0	0
	2 0	0		2 0	III
	3 0	I		3 0	I
	4 0	II		4 0	0
		2			1
SOUTH	1 0	I	SOUTH	1 0	I
	2 0	II		2 0	II
	3 0	IIII		3 0	0
	4 0	IIII		4 0	I
	1 I	II		1 I	II
	2 0	III		2 0	0
	3 I	IIII		3 0	I
	4 0	III		4 I	II
		2			2
EAST	1 0	0	EAST	1 I	II
	2 0	0		2 0	I
	3 0	I		3 0	0
	4 0	II		4 0	II
	1 0	0		1 0	0
	2 0	III		2 II	0
	3 0	0		3 0	II
	4 0	IIII		4 I	II
		0			0
WEST	1 0	I	WEST	1 0	I
	2 0	II		2 0	III
	3 0	II		3 0	I
	4 0	II		4 0	II
	1 0	I		1 II	II
	2 0	0		2 0	0
	3 0	II		3 0	0
	4 0	0		4 0	I
		0			2
		0/4			9
		(67)			(69)
		-62			

(viii) Herb-layer baboon food biomass sheets

TRANSSECT A: PCQ: 2 OBS: Int. accoba: 17M
 Date: 11/15/1981
 AREA: 4 2 CROWN: 2 HAS: _____

GRASSES

GRASSES	Height	Low	Stem	Flower	Other
Eragrostis	33	1	0	1	0
Poa	1	1	0	0	0

HERBS

GRASSES

GRASSES	Height	Low	Stem	Flower	Other
Pennisetum	1	1/4	0	1/3	0
Guzmania	102	3	5/4	0	1/2
Grass	1	1/3	0	1	0
Eragrostis	11	1/3	0	1/2	0
Mimosa	8	1/3	0	1	0

HERBS

HERBS	Height	Low	Stem	Flower	Other
Hibiscus	1	1/3	0	0	0
Oxycoccus	1	1/1	0	0	0
Rice	2	1/3	0	0	0
FSC	1	1/3	0	0	0
GOI	1	1/3	0	0	0

on the way to the field

[illegible]

(ix) Tree and shrub baboon food biomass sheets

[illegible]

(x) Large mammal count sheet

ECOLOGICAL MONITORING: LARGE MAMMAL COUNTS

Starting in April 1990, mammal counts will be introduced into ecological monitoring in order to give a measure of competition by other large consumers of food in the area, and also predation threat.

TRANSECT A: Count all individuals of the following species seen on the way to the transect via Rough Rock, while walking along the transect, and by scanning with binoculars to each side of Rough Rock (establish specific points from which to scan and keep to them each month).

TRANSECTS B AND D: Count from the junction of the school road with the high road when heading for White Rock, during the transect, and in scans with binoculars from the two best vantage points.

Add ALL sightings of large predators (lion, cheetah, leopard, wild dog) buffalo and elephants, with numbers and location, seen in the month.

TRANSECT: - <u>A</u>	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	1991	JAN	FEB	MAR
browsers:													
GOAT + SHEEP	-	-	-	670*	1650	770	-						-
GIRAFFE	5	4	1	-	3	1	-						
GERENUK	-	-	3	4	-	-	12						
mixed:													
ORYX	30	16	-	-	1	-	11						
ELAND	1	3	50	-	-	-	-						
grazers:													
KONGONI	-	15	9	-	-	-	21						
IMPALA	-	-	-	-	-	-	-						
GRANTS	14	2	-	-	-	-	-						
THOMMIE	-	44	25	29	1	-	40						
ZEBRA	53	82	36	3	11	-	75						
CATTLE	=	=	300	83 + 100	345	202	200						
digger:													
WARTHOG	11	4	16	6	6	8	1						
OTHER? <u>BA-Round:</u>	-	-	13	2	-	-	240						
<u>QUINCEA FAL:</u>	17	12	-	-	1000	-	-						
ELEPHANT													
(give details)	-	* ₁	* ₂	-	-	* ₃	-						
BUFFALO													
(give details)	-	-	-	-	-	-	-						
PREDATORS													
(give details)	-	-	-	* ₄	* ₅	* ₆	-						
TIME OF SURVEY	NOON	11:00	11:00	11:00	12:00	10:00	11:00						

* over page

*
See over

APPENDIX E

AD LIBITUM RECORD OF A WEANING TANTRUM

The following describes the behaviour of EI (a 10 month old infant) during a weaning tantrum which was in response to rejection by his mother, EU. (EU had at that time resumed cycling: WE is an adult male, frequently found in close proximity to EU).

8/1/90

14:35 EI squeaking and moaning beside EU, touching nipple with hand; holding nipple. Screaming when EU moves after she had been sitting for a while to eat Sans. int. [Sanseveira intermedia stem]. Approaching WE who is 6m away from EU, whimpering and moaning. Eating Sans. int. and still moaning; ignored by WE. WE moves. EI squeaks and stays sitting.

14:40 EI runs screaming to EU; squeaking and moaning as she walks; holds nipple; runs ahead of EU and squeaks; jumps away. Repeats all this. Sits and eats Sans. int., moaning. Screams and runs to EU. Sits in front of her moaning. EU moves. EI runs to her whimpering. EU eats Sans. int. EI sits in front of her and moans. EU moves. EI picks up discarded Sans. int. and eats it, screams and runs after EU. Walks beside her whimpering. EI is hit out of the way by EU, followed by great screams. EU sits and eats Sans. int.. Both walk, EI still screaming. EU sits and eats, EI still screaming. Repeats.

14:48 EI walking and screaming beside EU. EU sits. EI trying to hold nipple - arm stretched out. Walks on as before. Sits, EI trying to hold nipple - arm out. EI eats discarded Sans. int. moaning. Screams when EU moves. EI grooming arm and remains sitting. Runs to EU. Walking and screaming.

14:52 EI climbs on EU's back moaning (but less); riding jockey style.

14:53 Quieter. EI eats Solanum flower.

14:55 EU sits and EI comes off back. Walks quietly behind EU, feeding and sitting.

14:56 EI out of sight, not near EU.

14:59 EI feeding away from EU, trying to pull up Sans. int.. All quiet.

Typical of a long weaning tantrum is the persistence of EI, in following EU, getting close to her, attempting to touch her nipple, despite being ignored or even attacked by her. In this case the tantrum resulted in contact with the mother but not access to the nipple.

APPENDIX F

**LIST OF TOP TEN FOODS EATEN BY YOUNG INFANTS, OLDER INFANTS
AND YOUNG JUVENILES IN THE MONTHS JUNE - OCTOBER 1990**

June

Young infants

Mariscus amanropus/bases
Mariscus amanropus/scraps
Unidentified brown material
Acacia etbaica/seed (dry pod)
Euphorbia nyikae/scraps
Unidentified
Sanseveria intermedia/bases
Ipomea mambassana/fruits
Farsetia stenoptera/fruits
Sanseveria intermedia/scraps

Older infants

Mariscus amanropus/bases
Euphorbia nyikae/scraps
Unidentified brown material
Sanseveria intermedia/bases
Grewia tembensis/fruits
Mariscus amanropus/scraps
Lyceum europeum/leaves
Unidentified
Acacia nilotica/exudate globule on pod
Cocoon

Juveniles

Mariscus amanropus/bases
Euphorbia nyikae/pads
Sanseveria intermedia/bases
Grewia tembensis/fruits
Unidentified
Unidentified brown material
Ipomea mambassana/fruits
Acacia etbaica/seed (dry pod on ground)
Lyceum europeum/leaves
Invertebrate

July

Young infants

Mariscus amanropus/scraps
Mariscus amanropus/bases
Cynodon spp./leaves
Acacia nilotica./seed (fresh pod)
Acacia nilotica/seed (dry pod)
Ipomea mambassana/flowers
Acacia nilotica/seed (fresh pod on ground)
Opuntia vulgaris/scraps
Acacia nilotica/scraps
Acacia tortilis/seed (fresh pod)

Older infants

Mariscus amanropus/bases
Acacia nilotica/seed (fresh pod)
Acacia nilotica/seed (fresh pod on ground)
"Large" Ipomea/flowers
Acacia nilotica/seed (dry pod)
Mariscus amanropus/scraps
Acacia etbaica/seed (fresh pod)
Sanseveria intermedia/bases
Acacia tortilis/flowers

Juveniles

Mariscus amanropus/bases
Acacia etbaica/seed (fresh pod)
Acacia nilotica/seed (fresh pod on ground)
Acacia nilotica/seed (fresh pod)
Acacia nilotica/seed (dry pod on ground)
Sanseveria intermedia/bases
Acacia etbaica/seed (fresh pod on ground)
Unidentified
Euphorbia heterochroma/stem
Unidentified brown material

August

Young infants

Acacia etbaica/flowers
Acacia tortilis/flowers
Sanseveria intermedia/bases
Lyceum europeum/leaves
Euphorbia nyikae/scraps
Acacia etbaica/seed (fresh pod)
Acacia etbaica/exudate
Acacia tortilis/seed (fresh pod)
Unidentified
Acacia tortilis/seed (dry pod)

Older infants

Sanseveria intermedia/bases
Cynodon spp./leaves
Acacia tortilis/flowers
Acacia etbaica/exudate
Acacia etbaica/flowers
Euphorbia heterochroma/stem
Mariscus amanropus/bases
Acacia etbaica/seed (fresh pod on ground)
Lyceum europeum/leaves
Unidentified brown material

Juveniles

Sanseveria intermedia/seed (fresh pod on ground)
Acacia tortilis/flowers
Lyceum europeum/leaves
Acacia etbaica/flowers
Acacia etbaica/exudate
Euphorbia heterochroma/stem
Mariscus amanropus/bases
Cynodon spp./leaves
210/flowers
102/leaves

Adult females

Acacia tortilis/flowers
Cynodon spp./leaves
Lyceum europeum/leaves
Sanseveria intermedia/bases
Euphorbia nyikae/pads
Acacia etbaica/flowers
Euphorbia heterochroma/stem
102/leaves
Mariscus amanropus/bases
Euphorbia nyikae/scraps

September

Young infants

Acacia etbaica/flowers
Euphorbia nyikae/scraps
Mariscus amanropus/bases
Acacia etbaica/exudate
Acacia tortilis/flowers
Unidentified
Mariscus amanropus/scraps
Lyceum europeum/leaves
Grewia tembensis/fruits
Unidentified brown material

Older infants

Acacia etbaica/flowers
Euphorbia nyikae/scraps
Mariscus amanropus/bases
Grewia tembensis/fruits
Acacia tortilis/flowers
Sanseveria intermedia/bases
Acacia etbaica/exudate
Lyceum europeum/leaves
Euphorbia heterochroma/stem
Acacia etbaica/dry seed

Juveniles

Acacia etbaica/flowers
Sanseveria intermedia/bases
Lyceum europeum/leaves
Grewia tembensis/fruits
Acacia tortilis/flowers
Acacia etbaica/exudate
Mariscus amanropus/bases
Acacia etbaica/dry seed
Euphorbia heterochroma/stem
Euphorbia nyikae/pads

Adult females

Acacia etbaica/flowers
Euphorbia nyikae/pads
Euphorbia nyikae/scraps
Acacia etbaica/dry seed
Acacia etbaica/flowers on ground
Grewia tembensis/fruits
Acacia tortilis/flowers
309/fruits
Mariscus amanropus/bases
Lyceum europeum/leaves

October

Young infants

Acacia tortilis/flowers
Acacia etbaica/exudate
Cynodon spp./leaves
Mariscus amanropus/bases
Acacia etbaica/dry seed
Peressitum spp./leaves
Opuntia vulgaris/scraps
Unidentified brown material
Unidentified grass spp./leaves
Euphorbia heterochroma/tip

Older infants

Cynodon spp./leaves
Acacia tortilis/flowers
Mariscus amanropus/bases
Acacia etbaica/exudate
903/leaves
Acacia etbaica/dry seed
Peressitum spp./leaves
Euphorbia nyikae/pads
Unidentified brown material
Euphorbia nyikae/scraps

Juveniles

Cynodon spp./leaves
Peressitum spp./leaves
Acacia etbaica/exudate
352/leaves
Acacia etbaica/dry seed
Sanseveria intermedia/stem
Mariscus amanropus/bases
Acacia etbaica/flowers
Unidentified brown material
Unidentified

Adult females

Cynodon spp./leaves
Euphorbia heterochroma/stem
Acacia etbaica/dry seed
Acacia tortilis/flowers
Acacia tortilis/flowers on ground
Sanseveria intermedia/bases
903/leaves
Euphorbia nyikae/pads
Peressitum spp./leaves
Sanseveria intermedia/stem